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MORPHOLOGY AND BIOLOGY OF THE GREEN APPLE APHIS

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INTRODUCTION

Owing to the abundance of the green apple aphis (*Aphis pomi* De Geer) at all times in most apple-growing regions and to the serious outbreaks of the species at different places and in different seasons, the writers were instructed to make a careful study of its life history. It was thought best to study the embryology of the insect in order, if possible, to explain the high mortality of the eggs in certain cases, their wintering condition, and, among other things, the most suitable time to attempt their destruction. Eggs were therefore taken during the winter of 1913–14 and again during that of 1914–15. With the opening of the season of 1914 generation experiments were begun at the deciduous fruit insect laboratory at Vienna, Va., and carried throughout the summer, fall, and early winter until the last sexes and eggs of the year were obtained. The material obtained from these experiments and the eggs in hand were studied and the manuscript prepared for publication during the winter of 1914–15.

During the summer the writers were assisted by Miss Dorothy Walton, and for three months by Miss Meta Neuman. These young ladies prepared the mounts of much of the summer material.

NAME OF THE SPECIES

The green apple aphis was first described by De Geer in 1773 (1, p. 53)[1] as follows:

Aphis (pomi) flavo-virides, corniculis longioribus, pedibus antennisque nigrescentibus, Pomi.

After giving this brief description De Geer enters upon a discussion of the insect, describing the different forms and giving interesting observations on the life history. For so early an account this is a very complete one and is much more valuable than many of those of more recent date.

In 1775 Fabricius (2, p. 737, no. 19) redescribed the species as follows:

A. Pyri, mali.
Habitat sub pyri mali foliis.
Corpus viride, antennis pedibusque fuscis. Abdomen nec marginatum, nec plicatum. Anus terminator stylo nigro. Corniculi cylindrici, nigri. Variat corpore toto rufescente, pedibus fuscis et interdum pedibus lividis, geniculis fuscis.

This name, *Aphis mali* Fab., was that by which the insect was commonly known until recent years. There seems, however, little reason for having adopted it, as Fabricius himself in 1794 (3, p. 216, no. 29) gives De Geer's insect as synonymous with his. He, however, uses his own name "*mali*" for the species and disregards De Geer's "*pomi*" altogether. "*Mali*," then, became the accepted name for the species. Unfortunately in this country the name "*mali*" was for many years applied to an entirely different species, now known as "*avenae* Fab.," under the impression that it was the apple insect of Fabricius. This error was first introduced into the literature of this country by Fitch (5, p. 65), and the same author later (6, p. 753-764; repr. p. 49-60) gave a very good description of *avenae*, under the name "*mali*." In this, however, he was only following European entomologists, such as Walker (4, p. 269), who used the name "*mali*" for an entirely distinct aphis.

Later writers followed in the same path, some, such as Buckton (7, p. 44, pl. 50), even confusing several species under the name. Sanderson (10, p. 191) used the name "*padi*" for this species in 1901. In more recent years De Geer's name has been given preference, and in this country the descriptions of Smith (9) and Sanderson (11, p. 130) have fixed the species to which it should be applied. The insect herein discussed must then be known as "*Aphis pomi* De Geer."

[1] Reference is made by number to "Literature cited," p. 992-993.

HISTORY AND DISTRIBUTION

Apparently the earliest record of the green apple aphis is the description by De Geer (1, p. 53), who states, in connection with this description, that he made rather extended observations of the species during the autumn of 1746. He also states that the insects were very abundant on the apple (*Malus* spp.) and often killed young trees. De Geer's observations were made in Sweden. Since the original description, many other European records have been made, and the species is now known to occur in every country of Europe and at least as far east as Turkestan in Asia. Many writers have reported it as being very injurious, particularly to young trees.

The unfortunate confusion of names makes it impossible to determine to which species the earlier records in this country really pertain. By previous writers *pomi* has been considered of much more recent occurrence in this country than the other apple species, *avenae*. This opinion, however, is not well founded. Although the descriptions given by Fitch (5, p. 65; 6, p. 753–764; repr. p. 49–60) prove that he considered *avenae* to be the true *mali*, an examination of the material from the Fitch collection shows that part of his insects were *avenae* and part of them *pomi*, even as they might be collected to-day by one not knowing the differences between the species. The specimens of *pomi* are marked "showing variations," which would indicate that, although Fitch noted the differences, he did not consider them of specific value. This shows *pomi* to have been located in this country nearly as early as we have any definite records. It was taken in Washington State in 1883 and in the District of Columbia in the same year. Williams collected it in St. Louis in 1894, and in all probability the forms referred to as *mali* by Cowen in 1895, in the bulletin by Gillette and Baker (8, p. 120) were *pomi*, since he observed both winged and wingless insects on the apple on August 23. It was present in Illinois in 1897, and no doubt was well distributed over the country much earlier than we have heretofore supposed.

In 1900 Smith (9) published a life history of this species. His first definite observations were made in 1897, and he first separated the species from the *mali* of American authors. In 1902 Sanderson (11, p. 130) published life-history notes on the species under the name "*pomi* De Geer."

It is known that this species occurs throughout the country wherever apples are grown. The accompanying map (fig. 1) merely shows definite localities from which we have records of the insect. It would indicate that the species is most abundant in the East. This, however, is not the case, since various observers in the West record it as occurring throughout their States. It appears to be particularly abundant in Colorado and the neighboring States.

Aphis pomi also occurs in Canada, being found from Nova Scotia to British Columbia. It has recently been recorded in the Kootenai and Okanagan districts of the latter Province.

Outside of Europe and North America few records of the species occur. It is present in Japan (18) and Dewar (12, p. 12) records it from Orange Free State.

It is rather remarkable that this aphis has not become even more widely spread, since it is typically a nursery species and in the egg state is easily transported on nursery stock.

Both in this country and in Europe *Aphis pomi* is usually abundant and particularly injurious at irregular intervals. Thus, in 1911 a severe outbreak occurred in Virginia, while in 1912 the species was very abundant in New England and New York. Similar phenomena have been noted from Russia. In some portions of this country, however, it seems to be always present and injurious. Gillette and Taylor (14) state that in Colorado "*A. pomi* is one of our very worst orchard enemies."

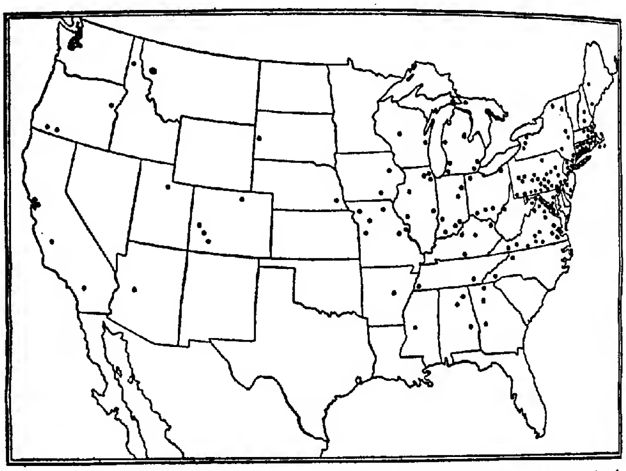

FIG. 1.—Map showing the localities in the United States from which the Bureau of Entomology has actual records of the green apple aphis (*Aphis pomi*).

METHODS OF STUDY

EXPERIMENTS.—In initiating the experiments on which the following paper is based, twigs which bore eggs were collected at the time the eggs were beginning to hatch. These were kept under close observation. As soon as an egg hatched, the young stem mother was transferred to another twig kept in a vial of water. Although fairly satisfactory at first, this method of handling the food soon proved to be undesirable. Therefore there were substituted, first, dormant seedlings which had

been kept in a cellar all winter, and later young green apple seedlings grown in pots. In handling the dormant stock the tops were cut off, leaving a stem of 4 or 5 inches, and growth was started by keeping the roots in water for 8 or 10 days before planting.

The plants were covered by lantern-globe cages—inverted lantern globes with cheesecloth fastened over the bottom by a rubber band.

After the first two weeks all work was carried on in an insectary all four sides of which were made of fly screen. This duplicated normal conditions very closely, except that in most cases the direct rays of the sun could not reach the plants during the middle of the day.

In the actual handling of the insects it was found that it was much better to transfer adults than young, as this transfer of adults could be accomplished much more quickly and with greater safety, there being less danger of breaking the beak of the mature insects. Consequently several generations were reared, one after another, on one plant. This was also of great advantage in studying the effect of a prolonged use of good or poor food.

The usual custom in rearing aphides appears to be to raise the first born from the first born and the last from the last throughout the season. Since it was desired to raise young from both wingless and winged mothers in every case, this method proved to be impracticable. Moreover, the opinion was held—an opinion which has been confirmed by the past season's work—that the thorough study of a species can not be accomplished by such methods, because too few insects are reared. Consequently, as many insects as possible were carried to maturity, the number varying between a few to 60 or more for each experiment. The winged forms were transferred to new plants as pupæ. The wingless form was reared to maturity, and then all but from one to three insects were removed, these few being allowed to reproduce. All molts and specimens of insects from each generation were mounted for further study. At first each individual molt was mounted on a separate slide, but later, as their number grew into the thousands, this was impossible and a series of molts was placed on each slide. The total number of experiments conducted during the season was 1,720, with an approximate total of 15,000 insects. These insects, together with their molts, thus gave us for study nearly 75,000 individual forms of known lineage. The study of these forms has been tedious, but it has been a valuable adjunct to the actual breeding, furnishing many data which would otherwise have been unavailable.

It should be understood that, while the method above outlined was followed as closely as possible, it could not, from local causes, be applied in every case. However, it has been found to be very satisfactory and is believed to be a more efficient method for a thorough scientific study of the life history of aphides than any that has been seen recorded.

TECHNIQUE.—For description, specimens were mounted in balsam in the usual way after having been dehydrated and cleared. Eggs were fixed with acetic-alcohol-sublimate solution, and after washing were preserved in 70 per cent alcohol. Those which had been preserved for some months gave better results on sectioning than did newly fixed material. Clearing was done in cedar oil, and sections from 5 to 10μ in thickness were cut; those 8μ gave the best results. Staining was done with Delafield's hematoxylin, orange G and picric acid, and Mayer's acid hemalum. Borax carmine was used for staining in toto.

THE EGG

DESCRIPTION

Size, 0.572 by 0.281 mm. Form oval, flattened on side next the bark; more or less covered with a glutinous substance which hardens with age. Color, glossy black.

The newly laid egg is not, as has been frequently stated for this species, yellowish green in color. It is a decided light-yellow, with rarely a slight tinge of green. It does, however, become somewhat greener during the change from yellow to black. This change is completed in the shade (insectary conditions) in from one to four days, usually a little over one.

The sterile egg can be easily separated from the fertile in that it is orange in color when laid. In one case such an egg finally turned to "ox blood," but this was the only example out of more than a hundred in which any color change took place before the egg began to shrivel up, at which time it sometimes became orange brown. This shriveling usually took place in about a week or 10 days after deposition.

LOCATION ON TREE

The green apple aphis hibernates only in the egg stage. The eggs are laid in the fall on the smooth twigs, and especially on water sprouts. They are apparently never laid on the trunks of the trees, or even upon the branches. This is to be expected, since the females feed continuously during the oviposition period, and they would be unable to obtain their food through the thick bark (Pl. LXXV, fig. 2).

Unless the eggs are very abundant, they are usually deposited around and under the buds and in wounds in the bark. When abundant, however, they will be found scattered promiscuously over the twigs, and in some cases these will be entirely blackened with them. It is very interesting to note that in the winter of 1914 a careful survey of a large bearing orchard near Vienna, Va., revealed the presence of eggs only on trees in the south to west portion, and they were most abundant in the southwest corner of the orchard. These results were duplicated in an examination of a small orchard of 4-year-old trees on the laboratory grounds. More-

over, in both of these cases, and also in examinations of many isolated trees, the eggs were found to be much more abundant on the southwest sides of the trees.

The eggs adhere so tightly to the bark that great care is needed in removing them, and often this can not be done without breaking them. On downy twigs it is impossible to remove the eggs without also removing some of the hairs which adhere to them. Neither alcohol nor xylol will dissolve the adhesive or free these hairs from the egg.

EMBRYOLOGY

GENERAL EMBRYOLOGY.—The substance of the unfertilized egg is very clearly divided into two areas. The first, comprising nearly all the space included within the vitelline membrane, is filled with the food yolk, which consists of homogeneous granules enmeshed in a fine network of protoplasm. The second area, filled with smaller granules, which the writers are calling the "ovarian yolk," following Webster and Phillips (17, p.95), is rather spherical in shape and lies at the posterior pole. Surrounding these two bodies is a very narrow layer of peripheral protoplasm, the periplasm or "*Keimhaut blastem*" in which the blastoderm will form later. The egg is included within two envelopes, the vitelline membrane and the chorion.

At the time of deposition the fertilized egg appears like the sterile egg. In a very short time, however, the production of cleavage cells commences, and the formation of the blastoderm is initiated. This begins at the anterior pole and progresses most rapidly in that region, but in a short time covers the entire yolk, with the exception of the posterior end, where it lies in contact with the ovarian yolk. A portion of the cleavage cells do not migrate to the periphery, but remain in the yolk to become yolk cells.

Invagination commences by a thickening of the blastoderm in its area of contact with the ovarian yolk, brought about by the division of the blastoderm cells along this area.

At the end of about five days the germ band attains a condition in which it rests or hibernates till early spring. In this resting stage the embryo occupies a position in the center of the egg, with its cephalic portion directed toward the posterior pole. The posterior half of the abdominal region is flexed dorsad in such a manner as to include the ovarian yolk. Segmentation is well advanced, and the formation of the appendages has begun. The stomatodeum and proctodeum are present, while the formation of the mesenteron has begun. The genital rudiments are separated into two groups, although the ovarian yolk is not yet divided. At the posterior pole lies an organ composed of a single layer of cells surrounding a pear-shaped orange body without structural characters. This has been designated by Webster and Phillips (17, p. 98) as the "polar organ."

Development is resumed in the late winter or early spring (March 12 to 15, during 1914 and 1915, at Vienna, Va.). Growth is not resumed uniformly, even in a group of eggs on a single twig, some starting two or three days before the majority and a few not beginning to grow till nearly the end of March. This renewed development is accompanied by a movement of the embryo through the yolk toward the posterior pole till that portion of the amnion which lies above the head comes in contact with the serosa at its junction with the polar organ. The two envelopes then rupture at this point and the embryo revolves about its transverse axis to its definitive position.

From this time on development is rapid. The serosa contracts, and is invaginated and absorbed. The appendages are completed, the development of the digestive tract is consummated; nervous and muscular systems are perfected. Within a period of from five days to two weeks, depending apparently entirely upon temperature conditions, the insect is ready to hatch.

Ovarian yolk.—At the posterior pole of the egg there is situated an almost spherical, dark-staining body. This has been termed the secondary yolk by most writers, but has been designated the "ovarian yolk" by Webster and Phillips (17, p. 95). The writers are unable to follow the formation of this body, as no egg material earlier than those eggs deposited by the female was preserved. Tannreuther (13) studied its formation in *Melanoxantherium salicis* L. He states that it is formed from the follicular nuclei of the oviduct wall, these dividing to form small vesicles which later unite and form common spherical masses. In the writer's earliest fertilized material (fertilized less than 24 hours) the ovarian yolk consists of a densely granular, almost spherical mass containing a number of large cells (Pl. LXVIII, fig. 7) which would correspond fairly well to the figures given by Tannreuther. At this time (Pl. LXVIII, fig. 1) the writers are unable to observe any cleavage cells within the body of the yolk, although there are at the anterior pole a number of dark-staining bodies well separated, but forming a dome-shaped structure conforming to the shape of the anterior part of the egg.

One thing is worthy of note in this connection. In unfertilized eggs, ranging in age from a few hours to 11 days, the ovarian yolk is a uniform, finely granular mass (Pl. LXVIII, fig. 3) without any of the large cells met with even in our earliest fertilized material. This leads to the belief that these bodies are associated with and appear only in connection with the beginning of growth. At the time the blastoderm is completely formed these bodies are present within the ovarian yolk and are surrounded by darker staining areas (Pl. LXVIII, fig. 2.) When the blastoderm is completely formed it covers the entire surface of the egg with the exception of the ovarian yolk, and invagination takes place about this yolk. (A single yolk cell is shown in Plate LXVIII, figure 6.)

It is thus carried to the interior of the egg with the developing germ band (Pl. LXIX, fig. 1). As the embryo develops, the ovarian yolk remains in connection with its posterior extremity, enlarges, and when this extremity becomes recurved, the yolk may be seen as a large, somewhat dumb-bell-shaped mass lying within the curve. At this time the large, deeply staining cells which form the end chambers of the ovaries are distinctly visible at its extremities. The remainder is a finely granular mass very similar in texture to that of the original ovarian yolk (Pl. LXIX, fig. 2). At a slightly later period the mass of the ovarian yolk becomes somewhat more enlarged in the heads of the dumb-bell at the expense of the "grip," and the end chambers are already forming (Pl. LXX, fig. 1). After the revolution of the embryo, the two heads of the dumb-bell-shaped yolk become separated, and it is henceforth represented by two large, slightly elongated masses, one on either side of the ventral portion of the body, the end chambers distinctly formed, and those on each side connected with one granular body of this ovarian yolk (Pl. LXX, fig. 2). In embryos almost ready to hatch, these two large granular bodies are still present, although more elongate than in the earlier stages. Some of the first egg chambers are now formed, and eggs may be noted within. The remainder of the reproductive organs are not yet developed (Pl. LXXI, fig. 1).

In the first instar of the stem mother these elongate granular bodies are still present. Webster and Phillips (17, p. 99) state that a group of cells which ultimately give rise to the generative organs separate off from the mesoderm during their "stage 6." The results of the present writers do not uphold this view. It seems more probable that these cells develop in the ovarian yolk, possibly from migrants, in the very early stages of growth, and that they are carried to the interior with this yolk at the time of invagination; that they here form two groups, one on either side of the ovarian yolk, which ultimately divides; and that these two masses of the ovarian yolk remain throughout embryonic development and assist in the formation of the reproductive system.

Polar organ.—Upon invagination the germ band leaves behind it, at the posterior pole of the egg, a group of large nucleated cells. This cell group has been recorded by Webster and Phillips (17, p. 98) as occurring in *Toxoptera graminum*, and was designated in their paper as the "polar organ." The writers have been unable to find any other reference in literature to the occurrence of such a body, either in the eggs of Aphididae or in those of any other insects.

The writers have not observed the genesis of this organ, but by the time the embryo has attained its "resting stage" it consists of a single layer of elongate cells surrounding a pear-shaped lumen (Pl. LXVIII, fig. 4). A large nucleus is present in the outer portion of each cell.

The lumen of this organ is occupied by a structureless yellow or orange-colored substance which extends by means of an elongated neck through an aperture in the chorion, thus opening upon the surface of the egg.

Webster and Phillips state that the yellow matter appears like a liquid. In *A. pomi* and in *A. avenae*, in which the organ is also present, it has more the appearance of a wax. Certainly it has a definite form which it maintains even when the surrounding cells are removed from it. The material is not affected by alcohol, xylol, or chloroform.

With the migration of the embryo to the surface and its revolution the cells of the polar organ are withdrawn, leaving the yellow body unchanged in form and still attached to the chorion. In one specimen which was in the late stages of development the yellow body was found inclosed by the anal portion of the embryo. Usually, however, it appears never to come in contact with the embryo; and when the latter hatches, it is left behind in the eggshell. The writers have been unable to find anything resembling it in any of the newly emerged insects.

Dorsal body.—With the resumption by the embryo of activities in the spring a change takes place in the cells of the polar organ. These flatten out, drawing away from the yellow mass as if the serosa were exerting an upward pull on them from all sides (Pl. LXVIII, fig. 5). Through the migration of the embryo the amnion finally comes in contact with the serosa at a point where the latter joins the cells of the polar organ, and both amnion and serosa rupture at this point.

As the embryo revolves, the serosa contracts until it lies as a thickened plate, the dorsal plate, near the anterior pole of the egg. In fact, in some cases the thickening takes place directly at the anterior pole, the plate moving later somewhat toward the posterior. During this contraction of the serosa it draws the cells of the polar organ after it, so that when the dorsal plate is formed, these lie as an irregular mass just posterior to the serosal cells (Pl. LXXI, fig. 2).

After the formation of the dorsal plate has been accomplished, this body commences to invaginate at its center, forming a tube which extends into the yolk ventrad, inclining slightly toward the posterior. This tube is formed of both the serosal cells and those which formerly constituted the polar organ. These cells can not now be distinguished from one another (Pl. LXXII, fig. 1).

This dorsal body soon separates itself entirely from the amnion and lies wholly immersed within the yolk in the form of a hollow sphere, one cell in thickness (Pl. LXXII, fig. 2). A little later this sphere breaks up and the cells disintegrate, probably being used as food by the embryo.

Resting stage.—From the standpoint of life history the resting stage is one of the most interesting points in the embryology of this species. The embryo appears to be very seriously affected by changes of temperature at this time, or rather by sudden changes to temperatures

higher than those normally occurring out of doors. Several lots of eggs containing "resting" embryos were taken into the greenhouse at Vienna, Va., during the winter of 1915.[1] The first lot was taken on January 7 and other lots were taken at intervals of from one to two weeks until after growth was resumed. All the eggs in all lots died within two weeks. Over 50 per cent of all eggs placed in the greenhouse after the revolution of the embryo commenced, hatched normally.

It was at first thought that humidity might be a factor in this mortality, but the following experiment eliminated that. A very hairy twig which was well infested with eggs was cut in two. One half was placed in water, just as it was. The hairs acted as a wick, drawing the water to the top of the twig and keeping it and the eggs constantly moist. The base of the other twig was cleaned so that the water could not reach the hairs, and it consequently was dry. Both lots of eggs began to hatch on the same day. Moreover, hatching proceeded a little more rapidly on the dry than on the wet twig. It should be stated that the eggs used in this experiment had resumed growth before being taken into the greenhouse. These results are confirmed by the fact that no difficulty was experienced in hatching eggs taken into warm temperatures after the middle of March.

It will be seen that the temperature effect upon the egg at this period is rather a complicated matter. The activities of the embryo in the spring are apparently initiated by a general rise in temperature above the normal winter average. It seems probable also that these higher average temperatures must continue for some time for this species, since warm weather of two or three days' duration, occurring in January and February, does not appear to induce any growth whatever in the embryo. Certainly there is no appreciable difference between embryos collected just before such a period and those collected after it.

On the other hand, if the temperature affecting the eggs is artificially raised to greenhouse temperature (about 65° F.) at any time before the normal resumption of growth, the embryo dies. It is true that in certain instances some activity is induced, and embryos treated in this manner will be found to have developed somewhat, but in no case in these experiments did the revolution of the embryo occur.

From data of the writers it would seem that the embryos need to pass through a period of cold weather, perhaps even need to be subjected to freezing temperatures. This is indicated by the fact that in eggs laid early in the season the embryos had reached the resting stage and ceased growth for three weeks or a month before later eggs were deposited. Yet these later eggs in their turn developed normally to the resting stage.

The amount of low temperature needed by the insect is very uncertain. As suggested previously, it may be that a single freezing is sufficient, or

[1] The average temperature in the greenhouse was about 65° F.

it is possible that continued cold weather, or a succession of freezings, is essential. In either case it seems probable that the embryo must have experienced a sufficient amount of low temperature long before spring and that it must thereafter continue to remain dormant till the proper average temperatures exist for its renewed activities. If, however, the embryos be subjected to temperatures well above the critical at any period before they have revolved, this change is fatal to them.

What this critical temperature is, can not be determined with any exactness from the data at hand. In 1915, from March 8 to 16, the period during which growth was resumed, the average temperature dropped to 34° F. only once, and it was below 36° only twice in the week. In 1914, however, the averages varied between 18° and 60° during what appears to have been the critical period, although from March 14 to 18, inclusive, it was above 34°. It seems probable that the critical temperature is close to 36°. Apparently, also, this critical temperature, or average temperatures a little above it, must continue for a period of some days, since frequently average temperatures higher than the critical occur for one or sometimes more days in January and February without affecting the insects.

It is interesting to note that eggs of *A. avenae* brought into the greenhouse during the winter hatched normally. Eggs of this species frequently hatch on the trees after warm spells of two or three days' duration in January and February; and while the writers have not as yet made a thorough study of the embryology of this species, yet during the winter they have taken several eggs in which the embryo had revolved.

These observations are of particular interest, since they undoubtedly explain the fact stated by several writers that a very low percentage—about 2 per cent, according to Gillette and Taylor (14, p. 24)—of the eggs of *A. pomi* hatch.

Hatching.—The first eggs hatched in 1914 about April 8 and the last about April 25. At this time nearly all the buds showed some green and in many cases the tiny leaves were free from the bud scales. Since it is as immature stem mothers that this and corresponding species are usually treated with insecticides, it will be well to include here a comparison of their dates of hatching. In the spring of 1914, at Vienna, *A. avenae* commenced hatching on March 28. *A. malifoliae* and *A. pomi*, however, did not hatch until about April 8. A few eggs of *A. malifoliae* hatched before that date, and this would seem to indicate that the rosy apple aphis is perhaps slightly earlier than the green aphis. For all practical purposes, however, their hatching dates are the same, while that of *A. avenae* is very much earlier.

The young stem mother emerges from the egg head foremost, and the latter is always split evenly over the vertex of the insect. This is accom-

plished by means of a bladelike egg burster, which extends from the region of the trophic tubercle over the vertex and backward on the crown as far as the posterior margin of the eyes (Pl. LXXIII). This egg burster is often armed with one or two toothlike projections on its cutting edge. After the shell has been ruptured, the young, still within the membrane, protrudes for almost its entire length before the membrane ruptures. It is not uncommon to find insects which have reached this stage and died. They stand upward almost out of the shell, but still within the membrane. After the membrane has become ruptured and the insect has emerged, the former position of the egg burster is indicated by a suture-like marking extending over the vertex and crown and separating the two halves of the dark-colored cap met with in the stem mother of this species.

PLAN OF DESCRIPTIONS

It has been found by the study of the different instars that the easiest method for separating them is by the character of the antennæ. By measurements of these organs it is possible to determine immediately the instar of the form examined. In describing the different stages, therefore, in the earlier instars, measurements of the antennæ only are given, and these are followed by a complete description of the adult form. In the third instar of the summer forms those insects destined to become pupæ can be distinguished from those destined to become wingless only by the presence of the beginning of the wing pads. The measurements for both are the same. For the first two instars, therefore, only one description is given. The pupæ of the intermediate and that of the winged form are the same in every respect, and, therefore, only one description is given for these forms.

It is often important to know, immediately on their hatching from the egg, to what species apple aphides belong. We give here, therefore, measurements of the antennæ of the first-stage stem mothers of the more common apple-infesting species which are likely to be confused—viz, *pomi*, the green apple aphis, *avenae* (Pl. LXXIV, fig. 15, 18), the apple-grain aphis, and *malifoliae* (Pl. LXXIV, fig. 17), the rosy apple aphis. The adult stem mothers of these species could hardly be confused, on account of their different color characters, but the newly hatched insects are most easily and definitely separated by an examination of the antennæ.

The relative lengths of the proximal and distal portions of the fourth antennal segment in the different species are given in Table I, and an examination of these figures will enable one to separate the species easily.

TABLE I.—*Lengths of third antennal segment and of proximal and distal portions of the fourth segment in Aphis pomi, A. avenae, and A. malifoliae*

Species.	Segment III.	Segment IV base.	Unguis IV.
	Mm.	*Mm.*	*Mm.*
Aphis pomi....................	0.08 to 0.09	0.048 to 0.056	0.048 to 0.064
Aphis avenae..................	.08 to .096	.03 to .048	.08 to .104
Aphis malifoliae...............	.128	.048	.048 to .16

It will be noted that *A. pomi* has a much shorter unguis than either of the other species and this at once distinguishes it.

STEM MOTHER

DESCRIPTION

FIRST INSTAR.—Morphological characters: Antennal segments (Pl. LXXIV, fig. 16) as follows: I, 0.032 mm.; II, 0.032 mm.; III, 0.08 to 0.09 mm.; IV, base 0.048 to 0.056 mm., unguis 0.048 to 0.064 mm.; segments III and IV imbricated and covered with a few stout spines, III armed with a distal sensorium, and IV with a sensory group at the base of the unguis composed of one large sensorium and several small ones. Eyes with 8 to 10 facets. Rostrum long. Cornicles short, thick, and rounded at the distal extremities. Cauda and anal plate rounded and densely setose. Legs with spinelike hairs.

Color characters: Body dark green (sometimes very dark) with appendages dusky; crown dusky to black with a median longitudinal uncolored suture-like stripe. Entire insect often slightly pruinose.

SECOND INSTAR.—Morphological characters: Antennal segments as follows: I, 0.032 mm.; II, 0.033 mm.; III, 0.08 mm.; IV, 0.048 to 0.064 mm.; V, base 0.048 to 0.064 mm, unguis 0.048 to 0.088 mm., usually about 0.075 mm.; segments III to V imbricated and with a few stout, spinelike hairs, IV with a distal sensorium similar to that on III of first instar, and V with the usual sensory group. Eyes with about 10 facets. Rostrum comparatively shorter than in first instar. Cornicles short and thick and rounded distad. Cauda and anal plate rounded and setose. Legs more slender than in preceding instar.

Color characters: Similar to the first instar, but lighter in color.

THIRD INSTAR.—Morphological characters: Antennæ much more slender than in the previous instars, with lengths as follows: I, 0.045 mm.; II, 0.042 to 0.045 mm.; III, 0.112 to 0.144 mm.; IV, 0.064 to 0.096 mm.; V, base 0.064 to 0.08 mm., unguis 0.088 to 0.112 mm., usually about 0.1 mm.; sensory characters as in previous instars. Eyes with over 20 facets; cornicles more elongate than in the other instars and not so rounded distad; cauda and anal plate rounded and setose.

Color characters: Similar to those of the previous instar.

FOURTH INSTAR.—Morphological characters: Antennæ fairly long and slender, with lengths as follows: I, 0.053 mm.; II, 0.048 mm.; III, 0.192 to 0.224 mm.; IV, 0.088 to 0.128 mm.; V, base 0.08 to 0.096 mm., unguis 0.112 to 0.128 mm.; segments III to V strongly imbricated, sensory characters as in other instars. Eyes with about 40 facets. Cornicles 0.153 mm. in length and imbricated. Cauda somewhat conical. Legs slender, tibiæ somewhat curved, 0.571 mm. long.

Color characters. Approaching those of the adult form.

FIFTH INSTAR (ADULT).—Morphological characters: Antennæ (Pl. LXXIV, fig. 5) rather long and slender, with lengths as follows: I, 0.06 mm.; II, 0.056 mm.; III,

0.296 to 0.416 mm.; IV, 0.16 to 0.192 mm.; V, base 0.096 to 0.12 mm., unguis 0.16 to 0.184 mm.; segments III to V imbricated and armed with several prominent spinelike hairs, segment IV with a distal sensorium, and V with the usual group. Eyes prominent and with very many facets, ocular tubercles distinct; lateral thoracic tubercles prominent; abdominal tubercles not so prominent. Cornicles cylindric, tapering, imbricated and sometimes slightly flanged, 0.288 to 0.368 mm. in length. Cauda narrow, conical, or very slightly constricted toward its middle, densely setose and armed with a few long curved hairs. Anal plate rounded, setose, and hairy. Legs slender, hind tibiæ 0.752 to 0.88 mm. long. Body quite globose, more so than that of summer form. Length, 1.92 mm.; width, 1.25 mm.

Color characters: General color green, somewhat darker than the summer forms; vertex and crown black; cornicles, cauda, and anal plates black, as are also the tarsi and the distal extremities of the tibiæ, femora, and labium; eyes deep brown. The entire insect is sometimes covered with a bloom.

LENGTH OF NYMPHAL LIFE

The newly hatched stem mothers spend the first day wandering about over the twig on which they were born, doing little or no feeding. They finally settle on the tiny leaves or in some instances on buds in which the green of the leaves barely shows. From this time on they feed almost continuously, seldom changing their positions unless the food is very poor. In that case they may wander about on the twigs. Such insects, however, are very likely not to settle permanently nor to live to reproduce.

The duration of the first instar of stem mothers averages from 4 to 5 days; that of the next three, 6 days, the time being equally divided among the three. The total nymphal life thus averages from 10 to 11 days. That the first instar is longer than the three others, and also longer than the first instar of later generations, is due to the fact that the young stem mother loses one or more days in searching for suitable food. Prolonged cold spells would undoubtedly retard this development somewhat, but the insects can withstand short spells of severe weather with little or no apparent effect. Poor food conditions would probably check their growth also, but this factor is negligible, since the same conditions which induce hatching also cause the buds to burst, so that the food is practically always ready for the insects. Moreover, as stated previously, insects which fail to locate good food, and wander about, seldom reach maturity.

REPRODUCTION

The stem mothers begin to reproduce in about 24 hours after becoming adult. In the experiments of the writers the greatest number of young produced by one stem mother was 42, during a period of 10 days. In most of the species which have been carefully studied the average reproduction by stem mothers is greater than that by any of the succeeding generations. Considerable difficulty was experienced in handling this

form, many of the aphides leaving the plants and dying before the reproductive period was finished. Consequently 42 young is probably below the average under natural conditions.

The young are produced in groups of varying numbers and with unequal periods between the groups. In a general way an adult will produce a group one day and rest the next, but often the rest period will be longer and sometimes shorter. Individual mothers vary greatly in their rate of reproduction from the average rate. Some stem mothers ceased to reproduce for 2 or 3 days between some groups, while others never rested long. The greatest number of young produced in 24 hours was 9, one insect producing this number at two different times. In 4 days 22 were produced by one mother. The average daily production was 4.2.

LONGEVITY

The greatest length of life observed was 20 days. This is undoubtedly much below the true maximum and probably somewhat below the average. In the case recorded the insect produced young up to the last day.

The first stem mothers were observed on April 8 and the last May 6. Under natural conditions this period may perhaps be a little longer.

SUMMER FORMS

NUMBER OF FORMS

Beginning with the second generation and continuing until the sexes were produced, the writers found three adult forms to be present. The most abundant form was the wingless viviparous female. This occurred in every generation, and, with the exception of the second, always outnumbered the other forms present. It would often appear, in definite lines of descent, for several generations without being accompanied by winged insects. In fact, one purely wingless line was carried from the stem mother to the sexes, although in this case winged forms sometimes occurred as sisters or cousins.

On the other hand, the winged form was much more abundant than seems to be the case in most of the other species which have been studied. Winged insects were obtained in every generation from the second to the sixteenth, inclusive, although they became rare after the thirteenth generation.

The third form, the intermediate, occurred in 16 experiments, the first occurrence being in the third generation and the last in the twelfth.

In all, there were from 7 to 17 generations of the summer forms, the number depending upon whether the first or the last young were taken as mothers in each generation. In view of the fact that we have found winged forms to occur so commonly, it is difficult to understand how Smith (9) could have come to the conclusion that no winged insects

occurred after the third generation, an error in which he has been followed by many writers. He also states that only seven generations of the summer forms occur, another error which has been frequently quoted.

WINGLESS VIVIPAROUS FEMALE (PL. LXVII, FIG. 5)

DESCRIPTION

FIRST INSTAR.—Morphological characters: Antennæ (Pl. LXXIV, fig. 4) as follows: I, 0.034 mm.; II, 0.036 mm.; III, 0.120 to 0.144 mm.; IV, base 0.064 mm., unguis 0.112 to 0.128 mm.; segments III and IV imbricated and armed with a few spinelike hairs, III with a distal sensorium, and IV with the usual sensory group at base of unguis. Eyes with 12 to 14 facets; cornicles short, thick and rounded distad; legs thick, hind tibiæ 0.239 mm. long.

Color characters: Color very variable from a light or dark green to yellowish. In some cases the insects are a golden yellow; the normal color is a medium green, never, however, as dark as the stem mother. Appendages dusky.

SECOND INSTAR.—Morphological characters: Antennæ (Pl. LXXIV, fig. 3) more slender than those of the other instars.; lengths as follows: I, 0.045 mm.; II, 0.046 mm.; III, 0.112 to 0.152 mm.; IV, 0.08 to 0.096 mm.; V, base 0.056 to 0.08 mm., unguis 0.144 to 0.176 mm.; segments III to V imbricated and with a few spines, IV with distal sensorium similar to that on III of first instar, and VI with the usual group. Eyes with 28 to 30 facets. Cornicles rounded at the distal extremity, thick and imbricated. Legs stout and covered with spinelike hairs, hind tibiæ 0.320 to 0.384 mm. in length. Cauda and anal plate setose, cauda somewhat conical.

Color characters: Similar to those of first instar.

THIRD INSTAR.—Morphological characters: Antennæ (Pl. LXXIV, fig. 2) rather long and slender; lengths as follows: I, 0.048 mm.; II, 0.051 mm.; III, 0.192 to 0.248 mm.; IV, 0.112 to 0.144 mm.; V, base 0.08 to 0.096 mm., unguis 0.2 to 0.232 mm.; segments III to V imbricated and bearing a few spines, the base of V strongly but regularly imbricated but the unguis quite regularly, so giving the appearance of almost complete rings; sensoria as in previous instar. Eyes with 38 to 40 facets. Cornicles slightly rounded at distal extremity, but not nearly as much as in previous instars, length about 0.188 mm. Legs more slender than in previous instars, hind tibiæ 0.448 to 0.054 mm. long. Cauda and anal plate setose, cauda bluntly conical.

Color characters: Similar to those of first instar.

FOURTH INSTAR.—Morphological characters: Antennæ (Pl. LXXIV, fig. 10) long and slender; lengths as follows: I, 0.62 mm.; II, 0.06 mm.; III, 0.144 to 0.192 mm.; IV, 0.134 to 0.176 mm.; IV, 0.152 to 0.192 mm.; VI, base 0.088 to 0.112 mm., unguis 0.248 to 0.304 mm.; segments III to VI distinctly imbricated and armed with a few prominent hairs, segment V with a distal sensorium (the original III of first instar now represents III, IV, and V). Eyes with about 58 facets. Cornicles rather slender, compared with the earlier ones, cylindric, imbricated, and about 0.264 mm. long. Hind tibiæ 0.672 mm. long. Cauda and anal plate setose, anal plate rounded, cauda bluntly conical.

Color characters: Similar to those of first instar. The appendages are here partly turned to the black color met in the adult form. The cornicles blacken from the distal extremity proximad.

FIFTH INSTAR (ADULT).—Morphological characters: Antennæ (Pl. LXXIV, fig. 1) long and slender compared with the early instars, but short compared with the body; lengths as follows: I, 0.064 mm.; II, 0.063 mm.; III, 0.224 to 0.320 mm.; IV, 0.176 to 0.240 mm.; V, 0.176 to 0.232 mm.; VI, base 0.104 to 0.128 mm., unguis 0.28 to 0.32 mm.; segments III to VI imbricated and with a few stout hairs; sensoria as in fourth instar. Vertex slightly rounded. Prothorax with a prominent tubercle on each side.

Abdomen with five distinct tubercles on each side, the one pair caudad of the cornicles and the most cephalic pair about equal in size and larger than the three median pairs. Cornicles (Pl. LXXIV, fig. 12) subcylindric, largest at the base, tapering slightly distad, slightly flanged at the tip and strongly imbricated, 0.398 mm. in length. Anal plate rounded, setose, and armed with about a dozen long curved hairs. Cauda (Pl. LXXIV, fig. 19) elongate, rounded distad, sometimes slightly constricted in the middle, setose, and armed on each side with about five long, curved hairs; length, about 0.176 mm. Legs slender, hairy, particularly the tibiæ; length of hind tibiæ, 0.837 mm.; hind tarsi, 0.112 mm.; length of insect from vertex to tip of cauda, 2.56 mm.

Color characters: General color very variable, from a light green to a very dark green. Head orange-yellow, sometimes with a purplish cast. This orange-yellow head is in many specimens much more pronounced than in others. Thorax similar to the head in color, shading off into yellowish green at the abdomen. Both head and thorax covered with a slight bloom. Abdomen light green. Antennæ yellowish, dark toward the tip; tarsi, cornicles, cauda, anal plate, distal extremities of femora, and proximal and distal extremities of the tibiæ black. Labium tipped with black. In specimens which have not been well supplied with food and which consequently are much stunted in growth, the colors are much deeper, the green being very dark over the entire body, whereas in well-fed, large specimens the color is light green. Late fall specimens which are exposed to low temperatures have a brownish cast.

OCCURRENCE

As stated previously, this was by far the most common form occurring during the summer. Moreover, in so far as the actual propagation of the species is concerned, it is the only summer form necessary, since we were able, without difficulty, to carry insects from the stem mother to the sexes without the intervention of a single winged individual. For the spread and consequently the greatest development of the species, winged summer forms seem necessary, since at the present time it has no other natural mode of becoming wholly disseminated. In nurseries the wingless insects may travel from tree to tree in the rows, and trees bearing eggs may be shipped to different parts of the world. Such dissemination, however, would be of little avail to a purely wingless species, as compared to one containing winged forms, since its attack thereafter would be confined to trees on which it was shipped, or at most to a few surrounding trees.

LENGTH OF NYMPHAL LIFE

The average duration of the nymphal period in this form was 7 to 8 days, the time being equally divided between the four stages. During the hot weather occurring in the last of June and first of July this period was shortened to 6 days, and in one instance an insect commenced reproduction when only 5 days old. On the other hand, with the beginning of cooler weather in the late summer the period exceeded this average. About September 1 the time occupied by the nymphal stages was from 8 to 9 days. This period gradually increased in length till the last of September, at which time it covered 11 days. During the month of

September the temperature dropped below 50° F. several times, reaching 37° in one instance. These extreme temperatures were of short duration, however, and the mean was never below 50°. By the end of October the nymph required 12 to 14 days to attain the mature condition. At times during this month the temperature averaged between 53.5° and 59° for periods of 24 to 36 hours. During such periods very little feeding or growth took place. The insects would stand perfectly motionless. Mechanical stimulus with a needle merely induced slight movements of one or two legs. Moreover, it required considerable time for the insects to recover from such conditions, and often maximum temperatures of 65° to 70° would not cause a resumption of active feeding.

The difficulty of exactly correlating the rate of growth with temperature conditions is greatly increased by the fact that the condition of the food supply was as great or even a greater factor in determining this rate of growth. This factor can only be appreciated, however, in marked cases. Usually the observer is unable to determine which of two plants offers the insects the best food, and consequently is unable to gauge the proper values of the two factors. The effect of the food condition is taken up more fully in another place (p. 983).

REPRODUCTION

As in the stem mothers, the wingless viviparous females begin reproduction about 24 hours after becoming mature. In fact, this condition obtained for all viviparous females, whatever the form.

The average reproduction varies greatly during the season and the writers find that their figures separate into three well-defined groups: First, reproduction by the summer forms born before July 1, and reproducing by July 6; second, reproduction by forms born between July 1 and September 1, beginning to reproduce between July 6 and September 10; third, forms born after September 1, commencing reproduction after September 10. Eighty wingless individuals in the first group produced an average of 55.4 young per insect; 113 wingless individuals in the second group averaged 30.9 young, while in the third group 24 wingless individuals averaged 12.1 young apiece. The last mothers of the season produced only from 1 to 4 or 6 young. The average reproduction per insect per day during the first period was 2.95, during the second 1.92, and during the third 0.83.

For the entire season the average per wingless insect was 37.5, and the daily average was 2.22. The greatest number of young produced by one individual was 133, while the maximum reproduction for one day was 16+, one insect producing 64 young in 4 days.

The rate of reproduction was very irregular. In some cases the majority of young were produced early in the life of the adult. In others comparatively few were produced during the first few days and then large

numbers were brought forth. Some insects bore numerous young daily till death; with others the production decreased gradually to that point; while in a third class the insects lived from 3 to 44 days after reproduction ceased, the longer period occurring in the fall, October and November. During the summer the longest period was 13 days. In one remarkable case an insect born on September 29 produced 10 young in 13 days (October 13 to 26). It then ceased to reproduce till December 5 (40 days), when it bore one young and died.

LONGEVITY

The average total length of life for the entire season was 30.9 days. This average is only for insects which reached maturity. Many died while still nymphs. The greatest length of life attained by one insect during the summer was 48 days. In the fall the average period was longer than in the summer, and one insect lived 68 days.

Wingless viviparous females were present on the trees until within less than a week from the time of the last appearance of oviparous females—i. e., during the fall of 1914 until after November 20. In the cages one insect was alive on December 22.

HARDINESS

A rather interesting note was made during the fall on the effect of low temperature on the activities of this species. On December 22 an examination of about 50 insects, including wingless viviparous females and oviparous females, showed all the insects to be perfectly motionless, except one viviparous female. This insect moved both legs and antennæ when irritated slightly with a camel's-hair brush. The temperature at the time the observations were made was 34° F. and had remained constant for about 2 hours. For the 12 hours previous the temperature had been 30° F. or less. This would indicate that at least in individual cases the developmental or physiological zero for this species is quite low.

WINGED VIVIPAROUS FEMALE (PL. LXVII, FIG. 1)

DESCRIPTION

FIRST, SECOND, AND THIRD INSTARS.—In the first and second instars these insects are identical in form with those producing wingless adults. In the third instar the measurements are the same for those given under third instar wingless female, but beginnings of wing pads are present.

FOURTH INSTAR (PUPA) (PL. LXVII, FIG. 3).—The pupæ producing intermediates and those producing winged forms are identical, as follows:

Morphological characters: Antennæ as follows: I, 0.06 mm.; II, 0.06 mm.; III, 0.176 to 0.256 mm.; IV, 0.128 to 0.176 mm.; V, 0.128 mm.; VI, base 0.80 to 0.112 mm., unguis 0.216 to 0.28 mm.; sensoria, imbrications, etc., as in the wingless form. Vertex rounded, with a slight median indentation. Eyes prominent, with a large number of facets; ocular tubercles distinct and with usually three lenses. Thoracic and abdom-

inal sutures as in the wingless form. Wing pads prominent, extending somewhat caudad of the hind coxæ. Cornicles subcylindric, imbricated, slightly flanged; length, 0.168 to 0.376 mm. Legs slender, hairy, hind tibiæ 0.504 to 0.64 mm. long. Anal plate rounded, setose and armed with hairs. Cauda (Pl. LXXIV, fig. 21) conical, not as in the adult form, setose, and armed with many long, curved hairs. Length from vertex to tip of cauda, about 2.6 mm.

Color characters: General color greenish; head and thorax orange-yellow with a rosy bloom, the reddish appearance of this increasing with age. Abdomen yellow-green. Antennæ yellowish, with the distal segments dusky. Wing pads brown, with black costal margins. Eyes, tip of labium, tarsi, and distal extremities of tibiæ and tarsi black; cauda lighter than abdomen, not black as in adult. Area between cornicles darker green than the rest of the abdomen. In some cases the margins of the thorax are light-straw color, almost white, venter usually lighter than dorsum.

Fifth instar (adult).—There is no distinct spring or fall migrant in this species. All the winged individuals occurring throughout the spring, summer, and fall have the same characters and are identical, except for variations bearing no relation to season.

Morphological characters: Antennæ (Pl. LXXIV, fig. 7) as follows: I, 0.064 mm.; II, 0.063 mm.; III, 0.192 to 0.312 mm.; IV, 0.144 to 0.288 mm.; V, 0.144 to 0.224 mm.; VI, base 0.096 to 0.128 mm., unguis 0.288 to 0.344 mm., segments III to VI imbricated and armed with a few hairs, III with a row of usually 6 circular sensoria (range 4 to 9). These sensoria form an even row along the segment and are of about the same diameter as the segment. They have a distinct double rim. Segment IV often without sensoria, although on some specimens there are as many as 3 on this segment near its distal extremity. Sometimes one antenna has sensoria here and the other none. Segment V with a distal sensorium, and VI with the usual group at the base of the unguis. Vertex slightly rounded, median ocellus protruding, lateral ocelli very close to the compound eyes; these eyes large and showing with distinct tubercles. Thoracic and abdominal tubercles as described for the wingless form. Wings with delicate veins; forewing with the media normally twice branched, but not uncommonly with it only once branched and in rare cases (approaching the intermediate) this represented by one vein only. Cornicles (Pl. LXXIV, fig. 11) subcylindric, tapering toward the tip, imbricated and slightly flanged; length, 0.192 to 0.352 mm. Anal plate rounded, setose, and armed with a number of long, curved hairs. Cauda elongate, slightly constricted in the middle, rounded at the tip, densely setose, and armed on each side with about 5 long, curved hairs. Legs slender; hind tibiæ 0.56 to 0.992 mm. long. Length from vertex to tip of cauda, about 2.5 mm.

Color characters: Head and thorax shining black, sutures yellowish; antennæ straw color at base, dark, almost black distad; eyes black; legs yellowish, with the distal extremities of the femora, the distal and proximal extremities of the tibiæ, and the tarsi black. Abdomen yellow-green, with the margins and a longitudinal median stripe darker green. Cauda and anal plate black. Labrum straw color, with tip dusky or black. Wings hyaline, veins brown, stigma smoky.

Most of the winged forms had the abdomen uniform green, but with the second winged generation another form appeared. The color of this is as follows: Head and thorax black, similar to the first winged generation; veins and stigma dark; abdomen unlike the uniform pea green of the first winged generation, but much darker, with a median longitudinal stripe of still darker green; margin of the abdomen on each side with a row of 5 or 6 dark patches; other characters as in first winged generation.

The color characters of this winged generation may have had something to do with the confusion of *A. pomi* and *A. avenae*, as the color characters of the two are quite similar.

CAUSE OF PRODUCTION

The theory has been frequently advanced that the production of winged forms during the summer is due to a lack of sufficient nourishment for the insects. In some cases the wording of this theory is modified by the statement that winged forms appear on plants which are very heavily infested. The writers' results are a flat contradiction of this theory for this species.

As has been stated previously, in handling the insects the writers always transferred the mothers to new plants, rather than the progeny. In this way several consecutive generations were reared on one plant. Thus the effect of poor or good food would be accentuated. Yet the winged forms were never obtained in series of small, poorly fed insects, but occurred frequently in well-nourished series.

It should be stated that these results are not based on deliberate experiments to obtain data on this point. Notes were made simply because of a very evident abnormality in size and rapidity of development, correlated with a lack or an abundance of food. Later, in studying the notes, it was found that the large, well-fed insects developed rapidly and often produced winged forms, while many of the small, starved aphides produced only wingless progeny. Moreover, none of the plants was heavily infested, so the production of winged aphides can not be correlated with that condition.

In addition to the foregoing data, it was found that those winged insects produced during the summer months showed little or no inclination to leave the plants on which they were produced. This would at once disprove the theory that these winged forms are produced when the insect meets adverse food conditions in order to carry it to better food.

Other writers have maintained that the winged insects were produced as the result of an abundance of certain chemicals in the soil. The writers' work would not certainly contradict this theory. Still, the fact that the soil used was mixed in large batches and that winged forms were produced on some of the plants, while other plants raised in soil from the same batch bore only wingless forms would seem to cast considerable doubt on its truth. It is also very difficult to understand how the occurrence of such a form as an intermediate could be made to conform to this theory.

The writers' results, deduced from very full notes on the life history of this aphis, lead to the belief that much of the evidence given in favor of these theories is based on insufficient data.

It seems much more probable, especially in view of the quite frequent occurrence of such a form as the intermediate, that the production of this winged form during the summer is merely a reversion from the wingless to the more primitive aphis form. As such it is doubtful whether food conditions have anything whatever to do with the matter.

OCCURRENCE

Although, as has already been stated, this form is not necessary for the successful propagation of the species, it occurs quite commonly throughout the greater part of the summer. In the second generation the winged form outnumbers the wingless, although the writers were unable to determine the exact proportion. Thereafter winged insects are always less abundant than wingless.

This form occurred, in the writers' experiments, in every generation from the second to the fifteenth, inclusive. It was of very rare occurrence, however, after the thirteenth generation. In the complete life-history diagram (fig. 4) it occurred 149 times, each occurrence representing a different combination of the two factors, form and generation, among the ancestors.

In the field winged forms were apparently present in small numbers all summer. Definite observations were made on several days during July and August. In all cases migrants were found in every colony of any considerable size.

It is very interesting to note that in only 18 cases were winged forms produced by winged mothers, and in only one case did three winged generations occur in succession.

The last winged insects were born on September 9; none were found after October, either in the experiments or on the trees.

LENGTH OF NYMPHAL LIFE

The immature stages of this form covered a period of two more days than did the same stages of the wingless form. This extra time was occupied in the pupal instar, the three earlier stages requiring the same amount of time as the corresponding stages of the wingless form.

REPRODUCTION

Dividing the season into periods similar to those used in the discussion of the wingless reproduction, the writers obtain the following figures: The average reproduction by 29 winged insects during the first period (to July 1) was 50.1 per mother; that of 25 insects in the second period (July 1 to September 1), 25.4 per mother. Very few winged insects occurred during the third period, and the writers have no complete records of progeny from any individuals. During the first period the average per insect per day was 2.92. During the second period it was 2.04.

The seasonal average production per insect was 39, while the daily average was 2.62. The greatest number produced in one day was 6, and the maximum number of young produced by one individual was 120 (in 21 days). The average length of the reproductive period for the entire season was 20.75 days.

LONGEVITY

The longest total life recorded for an individual of this form was 42 days.

FLIGHT

A large number of migrants of the second generation were reared on some small apple trees in the laboratory. These insects, on becoming adult, were very active, and several hundred were taken on the windows of the room in which they were confined. They were to a marked degree negatively geotropic. This was well illustrated by the fact that as many as 25 could be kept safely in a small open vial by simply holding it upside down. Almost without exception migrants transferred to new plants settled readily and made no attempt to fly farther. They were very likely to fly from the brush, however, during the process of transfer.

In the case of the later winged forms no such tendency toward flight was observed. In no case were winged aphides observed which had left the plants and clustered on the sides and tops of the cages, unless the plants were so nearly dead that the wingless forms also left them. Moreover, no particular caution was necessary in transferring them from one plant to another, since they showed no inclination toward flight. This would seem to indicate that the winged forms of the second generation alone correspond to the spring migrants of species with a definite alternation of hosts.

INTERMEDIATE FORM (PL. LXVII, FIG. 6)

DESCRIPTION

Morphological characters: Antennæ (Pl. LXXIV, fig. 6) as follows: I, 0.064 mm.; II, 0.064 mm.; III, 0.28 to 0.34 mm.; IV, 0.16 to 0.24 mm.; V, 0.144 to 0.208 mm.; VI, base 0.096 to 0.12 mm., unguis 0.176 to 0.328 mm. Antennal segments armed as in wingless individuals, with the exception of segment III, which is armed with unequal sized sensoria, varying from 4 to 6 in number. Vertex rounded; eyes with ocular tubercles present; ocelli absent, even from specimens with nearly half-size wing rudiments. Thorax and abdomen with tubercles as in the wingless form. Thorax not showing the distinct "corseletta" of the winged form, but indicating a series in these forms from the winged to the wingless condition. Wings of winged form represented here by reduced wings of about half the normal size, through gradations in different individuals until mere folds of the skin are seen. Cornicles subcylindric, tapering distad, imbricated, and slightly flanged; length, 0.272 to 0.496 mm. Anal plate rounded, setose, and armed with long hairs. Cauda elongate, slightly constricted in the middle, rounded at the tip, densely setose, and armed with five or six long curved hairs on each side. Leg slender, hairy; hind tibia 0.608 to 0.896 mm. long. Length of insect from vertex to tip of cauda, about 2.5 mm., but with much variation.

In general outline the intermediate conforms much more closely to the wingless insect than to the pupa, being plump and of regular outline without having the thorax sharply delineated.

Color characters: In color characters this form resembles the wingless female very closely. In most specimens the rudiments of the wings are of a light green color,

nearly the color of the abdomen, while in some others they are a dusky gray. In specimens that have wings as large as the normal hind wing of the winged form, these wings are transparent like those of the winged. In other color characters this form resembles the wingless female.

COMPARISON WITH USUAL FORMS

Up to and through the pupal stage these insects appear to be identical with the immature stages of the true winged aphides. In fact, the writers are not able to distinguish the pupal molts from which intermediates emerged from those shed by the winged insects.

The adults, however, more closely resemble the wingless individuals than the winged, in general bodily outline. They lose the "corseletta" of the thorax, which latter at the same time becomes less distinctly differentiated from the abdomen, conforming quite closely to the wingless form. The darker color is also lost, the head and thorax being concolorous with the abdomen.

Two indications of the winged character are retained, however. These insects bear rudiments of wings, varying from wings of nearly half size, with indications of some of the veins, to tiny pads which are hardly more than wrinkles of the skin. Also the antennæ of this form bear, on the third segment, sensoria like those of the winged insects, which are absent in the wingless form. These, however, are not normal, in that usually the entire six are not present, the numbers on the two antennæ vary, and the sensoria are not of uniform size, very few being as large as the normal ones.

One other interesting point is that the dorsoventral muscles of the thorax, which are developed in connection with flight, are very much reduced in all specimens and the longitudinal thoracic muscles are reduced in varying degrees, the amount of reduction in both cases coordinating quite closely with the reduction exhibited by the wings. The writers (19) believe these intermediates to be variants between the winged and wingless forms, and of perfectly normal occurrence, illustrating the steps by which the wingless condition has been attained in the Aphididae.

OCCURRENCE

Intermediates were of rather common occurrence, being observed, as stated above, in 16 experiments. In all, 31 individuals were found.

LENGTH OF NYMPHAL LIFE

The nymphal period was of the same length as that of the winged form. In fact it was impossible to distinguish between the two forms in any manner, until the adult condition was attained.

REPRODUCTION

Reproduction was perfectly normal. Both wingless and winged forms were produced, though the percentage of wingless forms was a little greater than by the wingless mothers. Three adults produced 81 young, an average of 27. This is much below the average for the other forms, but only 3 insects were used, and there is nothing to indicate that, normally, this form would not produce at least as many young as the winged mothers. The average daily reproduction was 2.13 for these three individuals, this being somewhat less than that of either of the other forms. Here, again, however, the small number of mothers detracts from the comparative value of the figures.

LONGEVITY

The average length of life for these three insects was 24.3 days, one living 27 days.

COMPARISON OF THE THREE FORMS

NYMPHAL STAGES

All three forms agree in having four immature stages, the first three existing for equal periods, while the last stage is about two days longer in the winged individuals and intermediates than in the wingless ones.

REPRODUCTION

Table II gives a comparison of the reproductive activities of the three forms.

TABLE II.—*Comparison of the reproductive activities of the three summer forms of Aphis pomi*

Form.	Number of insects.	Average per insect.				Average per day.				Maximum per insect.	Maximum per day.
		First period.	Second period.	Third period.	Season.	First period.	Second period.	Third period.	Season.		
Wingless	80	55.4				2.95					
Do.	113		30.9				1.92				
Do.	23			12.1				0.83			
Do.	217				37.5				2.22	133	16+
Winged	29	50.1				2.92					
Do.	25		25.4				2.04				
Do.	0										
Do.	54				39				2.62	120	6
Intermediate	3				24				2.13	27	5

It will be noticed that a comparison of the figures for the entire season gives the winged form a larger average reproduction per insect than the wingless. This is because no winged individuals occurred during the third period when the number of young produced was very low. Eliminating this factor we find that for the first two periods the average for wingless insects was 43+young, while for the winged aphides it was only 37.7. Unweighted averages have been used here, since it is desired to compare merely the production by the two forms under similar conditions, and the fact that wingless insects were so abundant during the second, or poorer, period would make the use of weighted averages unfair.

PRODUCTION OF SEXES

Both wingless and winged viviparous females may, in addition to producing viviparous females, produce the sexes. However, the wingless individuals are much more commonly sexuparous than the winged insects, since sexes were reared from only three individuals of the latter form.

DIMORPHIC REPRODUCTION

No exact data are available on which to base statements as to the prevalence of dimorphic reproduction—the production of two different forms by one mother. Nevertheless, enough data are at hand to show that it is of very frequent occurrence during the summer and may even be the rule. In several cases wingless, winged, and intermediate mothers produced both wingless and winged offspring. In many cases the first young produced were all wingless, while later progeny were winged; but this was not always true, since the very last young were sometimes wingless.

In a very few cases wingless mothers produced both viviparous and oviparous females, and in one or two instances both males and oviparous females. Again, in a few cases it was possible to determine that one mother produced both oviparous females and males, while in one instance a single viviparous insect produced viviparous females, oviparous females, and males. The production of oviparous females and males by the same mother is probably of quite common occurrence, but the dimorphic reproduction, including both agamic and sexual forms, appears to be rare. In the vast majority of cases one mother will produce only viviparous females or the sexes. It is of interest to note that in most of the cases recorded the agamic young were produced first and the sexes were the last forms produced by the mother.

OVERLAPPING GENERATIONS

Since the writers did not select the first and last young from each mother, they did not obtain exact data on the duration of each generation. However, using the average length of life of the various generations in

conjunction with their observations they can very closely approximate the true conditions.

In the diagram (fig. 2) the solid lines represent actual records. The hatched lines occurring at the beginning of the fifteenth to nineteenth generations are theoretical. They are necessitated by the fact that the earliest progeny was lost in some of these generations and it was necessary to continue with later offspring. The hatched lines at the end of the several generations are deduced by adding the average length of life to the date of last production of young.

It will be noted that theoretically all the generations from and including the seventh should be expected to produce the sexes. It is quite probable that such production occurs in nature, and that the sole reason sexes

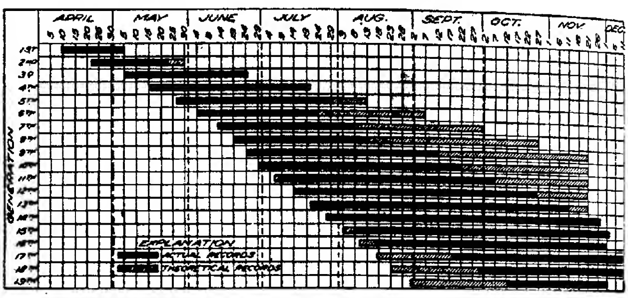

FIG. 2.—Diagram showing the overlapping generations of the green apple aphis.

were not obtained from the seventh, eighth, and ninth generations is that later members of these generations were not reared and bred from.

FEEDING HABITS

As noted previously, the stem mothers fed only on the exposed green of the bursting buds and tiny leaflets, as this was the only food available to them. Later generations preferred the leaf petioles and then the young, newly formed twigs, although some remained on the leaves. In cases where the latter were excessively downy, however, the young stages especially appeared to find some difficulty in living on them. This character of downiness seemed to be particularly unfavorable when occurring on the underside of the leaves. Later, when the twigs commenced to harden, the aphides migrated back to the underside of the leaves, and in the fall, at the time the sexes began to appear, practically no viviparous aphides were found in any other location on the trees. This selection of food occurred only when the numbers were comparatively small. In the case of excessive infestation, twigs, leaf petioles, and the underside of the leaves are attacked simultaneously. Occasionally a single aphis will be found feeding on the upper surface of a leaf, but these cases are so rare as to be almost negligible.

In the writers' experiments the feeding of this species caused very little leafcurl. In the field, however, it often induces considerable curling, and some writers have recorded the injury as being very severe. This injury appears to be produced mainly by the earlier generations. The writers have had under observation some old trees whose water sprouts were heavily infested from the middle of the summer to the close of the season. Very few of the leaves on these suckers showed any curling and these few were only slightly affected, being merely rolled over somewhat. Certainly the curling produced by this species (Pl. LXXV, fig. 1) is never as severe as that caused by *A. malifoliae*.

It is very interesting, in this connection, to note that in the spring we seldom found large, pure colonies of *A. pomi* occurring on the trees. In practically every instance there were some individuals of *A. malifoliae* present. Since a single half-grown stem mother of the latter species can cause very severe curling it seems probable that many of the records of this effect from the feeding of *A. pomi* should properly be referred to the rosy apple aphis.

This species has been reported as attacking and injuring young fruit in some cases, and in severe infestations young aphides are often found clustered on the apples. A few experiments were performed along these lines, but the insects could not be induced to feed on the fruit in any instance, even when all foliage was removed from the twig. It seems very probable, therefore, that such feeding is rather rare.

The quality of the food has a very marked effect upon the size, color, and rapidity of growth of the insect (Table III). When furnished with tender succulent food throughout larval life, the adults are large, plump, and light green in color. On the other hand, if the food is poor in quality, the adults will be smaller, dark green, and the bodies will be much wrinkled. The insect will also require a considerably longer period to attain maturity on poor food.

TABLE III.—*Effect of food on rapidity of development and reproduction of Aphis pomi*

Poor food, insects small.				Good food, insects large.			
Experiment No.	Date born.	Nymphal period.	Number of young produced.	Experiment No.	Date born.	Nymphal period.	Number of young produced.
		Days.				*Days.*	
1559	Aug. 5	10	15	1617	Aug. 13	7	....
1643	Aug. 14	10 to 12	8	1687	Aug. 19	7 to 8	28
1645	...do....	10 to 12	14	1839	Sept. 1	7 to 8	20
1488	July 28	11 to 13	44	1754	Aug. 21	7 to 8	25
1660	Aug. 17	12+	....	1807	Aug. 27	7 to 8	25
1852	Sept. 10	12 to 14	....	1856	Sept. 2	8 to 9	23
Average		11.5	10.25			7.7	24.2

It will be noted that in general the smaller forms occurred earlier in the year than the large ones, at a time when the average length of the nymphal period was particularly short; also that, while the percentage of young produced by the larger insects is below the seasonal average, it is, on the whole, higher than the average of the period in which the insects occurred.

It is very difficult to judge exactly the condition of the food supplied to the insects. The size of the leaves furnishes no criterion as to the amount of food available. The aphides do as well on young, newly opening leaves as on larger ones. In fact the largest, plumpest aphides reared were fed on such foliage, while the poorest conditioned insects were raised on old, dark leaves, whose general condition can perhaps best be described as "hard."

Some of the dormant trees used in the spring continued to live throughout the season. These furnished very satisfactory food at first. They put out slender twigs which never hardened and the leaves of which never fully unfolded. During the latter part of the summer, while the foliage continued perfectly green and appeared to be very succulent growth practically ceased. Aphides confined on these plants grew slowly and never attained the size or plump condition of the average adult.

SEXES

OVIPAROUS FEMALE (PL. LXVII, FIG. 4)

DESCRIPTION

FIRST INSTAR.—Morphological characters: Antennæ as follows: I, 0.025 mm.; II, 0.032 mm.; III, 0.096 to 0.128 mm.; IV, base 0.042 to 0.056 mm., unguis 0.088 to 0.12 mm.; segments I and II with stout spinelike hairs, III and IV imbricated and bearing similar spines; segment III with a distal sensorium, and IV with the usual sensory group. Compound eye with about 14 facets. Labium about as long as the antennæ. Legs hairy, hind tibiæ about 0.209 mm. long.

Color characters: Very variable, usually an olive green, with dusky appendages.

SECOND INSTAR.—Morphological characters: Antennæ as follows: I, 0.028 to 0.042 mm.; II, 0.028 to 0.042 mm.; III, 0.06 to 0.112 mm.; IV, 0.048 to 0.08 mm.; V, base 0.058 to 0.08 mm., unguis 0.12 to 0.16 mm.; segment IV with a distal sensorium, and V with the usual sensory group, otherwise quite similar to antennæ of last instar. Compound eyes with about 24 facets. Labium nearly as long as III and IV of the antennæ. Cornicles thick, rounded at the tip. Legs more slender than in the previous instar; length of hind tibiæ, 0.256 to 0.32 mm.

THIRD INSTAR.—Morphological characters: Antennæ as follows: I, 0.048 mm.; II, 0.048 mm.; III, 0.16 to 0.176 mm.; IV, 0.109 mm.; V, base 0.08 mm., unguis 0.184 to 0.208 mm.; segments armed similarly to those of the previous instar. Compound eyes with many facets. Cornicles more cylindric than in the previous instars, 0.112 mm. long. Legs slender, hind tibiæ 0.112 mm. long.

Color characters: As in previous instars.

FOURTH INSTAR.—Morphological characters: Antennæ as follows: I, 0.048 mm.; II, 0.048 mm.; III, 0.096 to 0.16 mm.; IV, 0.08 to 0.152 mm.; V, 0.096 to 0.144 mm.;

VI, base 0.08 to 0.096 mm., unguis 0.192 to 0.256 mm.; segment V with a distal sensorium, segments III to V imbricated and with a few prominent spines. Compound eyes large and with very many facets. Cornicles cylindric, 0.161 mm. long, imbricated. Legs slender, hind tibiæ 0.537 mm. long. Cauda conical, this and the anal plate densely setose.

Color characters: Approaching those of the adult, the dark green transverse band apparent in some cases, and the black portions more strongly developed than in the previous instar.

FIFTH INSTAR (ADULT).—Morphological characters: Antennæ as follows: I, 0.064 mm.; II, 0.064 mm.; III, 0.176 to 0.192 mm.; IV, 0.112 to 0.16 mm.; V, 0.144 to 0.176 mm.; VI, base 0.096 mm., unguis 0.24 to 0.288 mm.; segments III to VI imbricated and with a few rather prominent spinelike hairs, without sensoria excepting the usual distal one on V, and the sensory group at base of unguis. Vertex very slightly rounded. Compound eyes large, with distinct ocular tubercles; prothoracic tubercle very large and distinct; abdominal tubercles small with the exception of the first cephalic pair and the pair caudad of the cornicles. Cornicles (Pl. LXXIV, fig. 14) subcylindric, tapering distad, imbricated and slightly flanged. Legs slender, and armed with stiff hairs. Hind tibiæ slightly curved, very little, if at all, swollen, and armed with circular sensoria; these vary greatly in number, from a few to about fifteen (Pl. LXXIV, fig. 20). Three or four seem to be more common than the large numbers. They are very irregular in size, and are often very faint. Anal plate rounded, densely setose, and covered with a few long curved hairs on each side. Cauda somewhat elongate, conical setose, and armed with six or seven curved hairs on each side; length, 0.16 mm. Length of insect from vertex to tip of cauda, about 1.8 mm.

Color characters: Vertex and top of head dark brown to black. Thorax yellowish green, slightly pruinose. Anterior portion of the abdomen olive or greenish yellow, that portion just between and anterior to the cornicles dark green, forming quite a distinct band; segments of the abdomen caudad of the cornicles olive or yellowish green; margin of the abdomen with a row of dark markings. Cauda, anal plate, and cornicles black. Tarsi and distal extremities of tibiæ, femora, and antennæ dark brown.

In older specimens which have oviposited, the green band upon the abdomen becomes narrow and in very old specimens the body color often shows dark (dull) red-brown with the transverse band brighter than the remainder of the body. In a few cases the female is not olive or yellowish green as described, but is orange-yellow, of a color very similar to that of the males.

MALE (PL. LXVII, FIG. 2)

DESCRIPTION

FIRST INSTAR.—Morphological characters: Antennæ as follows: I, 0.024 mm.; II, 0.032 mm.; III, 0.096 mm., IV, base 0.056 mm., unguis 0.088 mm.; segments I and II with a few stout bristle-like hairs; segments III and IV imbricated, the third one toward its distal extremity only and both with a few stout hairs; segment III with a distal sensorium, and IV with the usual group at the base of the unguis. Compound eye with 12 to 14 facets. Cornicles short, thick, and rounded at their distal extremities. Labrum about as long as segments III and IV of antenna. Legs thick and very hairy, hind tibiæ 0.19 mm. long.

Color characters: Pale yellowish brown with dusky appendages and with the body often covered with a mealy bloom.

SECOND INSTAR.—Morphological characters: Antennæ as follows: I, 0.024 mm.; II, 0.032 mm.; III, 0.064 mm.; IV, 0.056 mm.; V, base 0.048 mm., unguis 0.096 mm.; segments with the characters of first instar, excepting that the distal sensorium is on segment IV. Compound eyes with about 18 facets. Cornicles short. Legs somewhat similar to those of the previous instar, hind tibiæ 0.192 mm. long.

Color characters: Similar to those of the previous instar. Tarsi, distal extremities of tibiæ, and distal extremities of antennæ black.

THIRD INSTAR.—Morphological characters: Antennæ as follows: I, 0.032 mm.; II, 0.04 mm.; III, 0.112 mm.; IV, 0.08 mm.; V, base 0.064 mm., unguis 0.112 mm. Armament of the antennæ, legs, etc., as in previous instar.

Color characters: As in previous instar.

FOURTH INSTAR.—Morphological characters: Antennæ as follows: I, 0.041 mm.; II, 0.041 mm.; III, 0.08 to 0.144 mm.; IV, 0.056 to 0.128 mm.; V, 0.072 to 0.112 mm.; VI, base 0.064 to 0.08 mm., unguis 0.128 to 0.176 mm.; segments III to VI imbricated and armed with a few stout hairs; segment V with a distal sensorium and VI with the usual group at base of unguis, otherwise the segments are similar to those of previous instar. Compound eyes with very many facets. Cornicles cylindric and imbricated, 0.072 to 0.096 mm. in length. Legs with many prominent spines, tarsi imbricated, tibiæ 0.368 to 0.448 mm. long.

Color characters: General color characters similar to those of third instar. Black marking only on the distal extremities of the antennæ, the distal extremity of the labium, the cornicles, the tarsi, and the distal extremities of the tibiæ.

FIFTH INSTAR (ADULT).—Morphological characters: Antennæ (Pl. LXXIV, fig. 9) as follows: I, 0.045 mm.; II, 0.045 mm.; III, 0.16 to 0.184 mm.; IV, 0.128 to 0.168 mm.; V, 0.112 to 0.144 mm.; VI, base 0.081 mm., unguis 0.184 to 0.232 mm.; segments III to VI strongly imbricated and armed with numerous stout hairs; segment III with 7 to 10 irregularly placed sensoria, the arrangement of these giving the segment a slightly knotty appearance; segment IV with about an equal number of sensoria irregularly arranged; segment V with about 5 sensoria of unequal size and with irregular arrangement; segment VI with the usual group at the base of the unguis. Vertex slightly rounded. Eyes with distinct ocular tubercles; thorax with a very prominent tubercle; abdomen with four lateral tubercles on each side, the pair caudad of the cornicles and the most cephalic pair larger than the others. Cornicles (Pl. LXXIV, fig. 13) cylindric, imbricated, slightly flanged distad, 0.104 to 0.28 mm. in length. Legs slender, hind tibiæ 0.496 to 0.592 mm. long. Cauda conical, not constricted, setose, and armed with long curved hairs. Anal plate somewhat truncate; genital plate rounded, wrinkled, and spiny; claspers irregular, corrugated, covered with minute spines; penis long, curved, fleshy (Pl. LXXIV, fig. 8). Length from vertex to tip of abdomen, about 1.12 mm. Shape of insect elongate and narrow, much more so than any other form.

Color characters: General color greenish brown, occasionally olive, sometimes with an orange tinge. Antennæ, cornicles, cauda, and genital appendages black; crown with a black cap similar to that of the stem mother; tip of the labium smoky to black. Insects sometimes slightly pruinose.

FIRST APPEARANCE OF SEXES

The production of the sexes is governed apparently by two factors, the season (temperature being of prime importance in this factor) and the generation. Of these the first is by far the more important.

The earliest sexes in breeding cages were born on September 2. They were in the eleventh generation, which was also the earliest generation in

which they occurred in the experiments.[1] Yet some viviparous insects of the sixteenth generation had been born as early as August 17, indicating very clearly that the season is of great importance in determining the production of sexual forms.

The evidence supporting the other factor is not quite so direct. The first sexes in the eleventh generation were born on September 2, in the twelfth and thirteenth, on September 5; in the fourteenth, on September 8; in the fifteenth, on September 22; in the sixteenth and seventeenth, on September 24. In all the generations up to and including the fifteenth, viviparous young were born on or before September 3.[2] In the sixteenth generation no young were produced between September 3 and 9, when viviparous young were born. The earliest vivipara in the seventeenth generation were produced on September 19.

The accompanying diagram (fig. 3) gives the curves for percentage of experiments containing sexes, by dates. Each date summarizes the production for seven days, the recorded date being the middle one of the seven. The writers can not give the exact percentage of sexes in each generation, since all of the progeny were not reared. However, of the generations occurring wholly after September 1, the sixteenth contained sexes in 51 per cent of the experiments, the seventeenth in 80 per cent, and the eighteenth in 100 per cent. In the nineteenth generation all the insects produced were oviparous females or males.

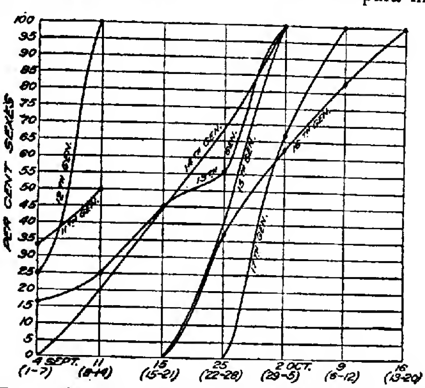

FIG. 3.—Diagram showing curves for percentage of experiments on the green apple aphis in which the sexes appeared.

The most striking points brought out by these figures are that, besides the fact that each generation first occurs at a later period than its predecessor, an additional period is required (to and including the seventeenth generation) for the first appearance of sexes, and that in general the earlier generations are producing sexes in every experiment at a time when later generations are producing them in a very small percentage of experiments. This would indicate that, while seasonal climatic con-

[1] It seems probable that they may occur as early as the eighth generation under some conditions. See page 982.

[2] The insects born in the sixteenth generation before August 17 are not included in this discussion, since they failed to reach maturity, and it was necessary to go back two generations for new material.

ditions are the principal factor in the production of these forms, yet different, perhaps more severe, conditions are needed for each succeeding generation. Also, the generation itself becomes of more and more importance, till in the eighteenth (first produced on September 30) every experiment contains some sexes, while in earlier generations batches of young containing only parthenogenetic females were produced after that date. This latter point is emphasized by the fact that in the nineteenth generation only sexes appeared, while in the earlier generations some viviparous insects were produced as late as were any of the insects in the nineteenth.

It should be stated that the first sexes, in the open, were observed about September 15. These were partially grown. By September 22 adult and nearly full-grown males and females were abundant, indicating that these forms were produced at least as early as the 6th of September.

PERCENTAGE OF MALES TO FEMALES

Notes were not made in every case of the numbers of males and females in an experiment, but the records of 71 experiments in which such figures were kept give an average of 11 per cent of males in a total of 350 insects. This is above the true average, since many experiments contained "many females and no males," and such records have not been included. In only four experiments did the males outnumber the females, and in these experiments the greatest number of sexes raised was six.

LENGTH OF NYMPHAL LIFE

The period covered by the nymphal life of this form was considerably longer than that covered by the same stages of viviparous females, although there were only four nymphal stages, as in those forms. The average period for the immature stages was 20.6 days, the range being from 16 to 36 days. It was impossible to obtain satisfactory data as to the divisions of this period occupied by each stage, as in the majority of the oviparous females the normal rate of growth was considerably deranged by cold spells. Such conditions would greatly retard the development of the insect, with the result that the particular stage in which the insect passed through such temperatures was lengthened in comparison with the other stages. Thus, one experiment might show the first to be the longest stage, while in another the longest stage might be the third. In the case of oviparous females born early in September, the first three stages occupied about the same amount of time as the entire nymphal period of the viviparous females, while the last stage continued for about 6 days. Later in the fall it was impossible to make a comparison. The males require the same amount of time for complete development as do the females and the length of the nymphal period is affected by climatic conditions in exactly the same manner for both sexes.

LONGEVITY

The longest record we have for total life of females is 47 days. At the end of this period the experiment containing two females was set aside and was not examined again for a month. At this time all were dead. The average life for the sexual females is about 25 days. The period varies with climatic conditions, insects born late in the season not living as long as those born in September. The total life period of the male appears to be considerably shorter than that of the female. The longest period observed was 31 days. In this case the male was never transferred from the plant on which it was born, and several females were present. When a male was transferred to a new tree bearing only one or two females, it usually disappeared within a week. In some cases it died, but often it could not be located at all. Toward the end of the season females were still quite abundant, but no males could be found.

The last oviparous females were observed, under natural conditions, on November 27. They were on a tree which still bore five or six green leaves. The next day these leaves fell and no more insects could be found. In the cages living oviparous females were present on January 5, at which time all experiments were closed.

HARDINESS

This species, particularly the oviparous females, can withstand very severe temperatures. On January 5, 1915, observations were made on some experiments in the insectary. These experiments contained both viviparous and oviparous females. At this date all the viviparous and most of the oviparous females were dead. However, on one plant one living insect was found, while a second plant bore six insects which were alive. These latter six were very quiet, showing only the slightest movement when disturbed. The other one, however, was quite active and moved about on the plant. At the time the observations were made (2 p. m.) the temperature was 43° F., and these insects had been subjected to such low temperatures several times, the minimum being -6°.

TING

The oviparous females may mate within two days, and possibly in ss time than that, after reaching maturity. On the other hand, a male may mate for the first time at least eight days after having ecome adult. The principal factor in determining this point is the cility with which the male finds the female.

Males have lived for considerable periods of time, as much as 10 days, nd have spent much of the time on the same leaf with the female, and et mating apparently did not take place. When males have been placed

beside females, even in contact with them, they have shown no signs of recognition. Sometimes they would remain by the female and commence feeding. Usually they would immediately wander away. Nevertheless, the male appears to be constantly searching for the female. Although it feeds considerably at periods, it is usually engaged in running rapidly about over the plant. The writers have seen such a male pass close to a female, which has produced one or more sterile eggs, several times and not pay the slightest attention to her. Some time later such a female would produce fertile eggs, proving conclusively that he finally found her. It may be that the female is only in condition to mate at certain times and that when not in condition she offers no attraction to the male.

The writers have never witnessed the entire act of copulation. A pair may remain in copula for at least 25 minutes, but whether or not the period is usually much longer than that is uncertain. During mating the female may move about carrying the male with her. She usually remains quiescent, however, with her beak inserted in the leaf or twig on which she rests.

Whether or not plural mating is necessary for fertilization of all the eggs is a point concerning which the writers are uncertain. It is indicated, however, by the fact that in a few cases females have laid fertile eggs and later sterile ones. Certainly plural mating takes place quite frequently. In one case under observation a female mated three times before laying any eggs, the first egg being produced between three and four days after the last mating observed. This is very difficult to explain unless the suggestion that the female mates only when in the proper condition is incorrect, in which case it is possible that the eggs were not fertilized by the first two matings. The writers have never observed females in copula after they have laid fertile eggs, but aphides which have laid sterile eggs frequently mate and produce fertile ones later.

OVIPOSITION

The shortest time observed by the writers to elapse between mating and egg deposition is 2 days. However, in one experiment a female deposited a sterile egg on one day and a fertile one on the next. This would suggest very strongly that oviposition may take place within 24 hours after mating.

In the experiments the number of eggs laid by females ranged from 1 to 6. The normal number appears to be 6, though the average was 4.75. The rate of deposition is very irregular. In one case a female laid 2 in 24 hours and a third in the next 48 hours. In another case a female produced 3 eggs which were laid 6 and 5 days apart. In several cases females which had been observed in copula produced no eggs whatever, although living several days afterwards. On the other hand

most of the unfertilized females were observed to produce some sterile eggs, frequently laying the entire 6.

During the fall of 1914, eggs were first observed on the trees at Vienna, Va., on September 29. These were newly laid, being still yellow in color.

SUMMARY OF LIFE HISTORY

The life history of *Aphis pomi* may be briefly outlined as follows: The egg is laid upon the tender twigs of the apple, though occasionally it is laid upon the bark of the older twigs. It is light yellow when laid, but later changes to shining black. Development for a few days is very rapid, after which the egg rests for the winter. When the revolution of the embryo is completed in the spring, an increase in temperature will cause the egg to hatch. Before this revolution a high temperature only tends to destroy it. Early in April the egg hatches by a uniform splitting over the insect's head.

The stem mother is wingless and becomes mature in about 10 days. She produces summer forms, both winged and wingless, with the winged ones predominating. There are 9 to 17 generations of the summer forms at Vienna, Va. After the second generation the wingless forms always outnumber the others, but winged forms may occur in every generation. They become rare toward the end of the season. On the other hand, a wingless line may be carried from the stem mother to the egg. A third form, the intermediate, may occur throughout the summer.

The wingless sexes begin to appear about the 1st of September. They occur in all generations, from the eleventh to the nineteenth, inclusive, and probably also in the ninth and tenth.

The summer wingless forms and the oviparous females, which live longer than the males, remain on the trees at Vienna, Va., until the leaves drop, usually about the middle to the last of November.

Mating commences toward the close of September, one male usually serving more than one female. Both sexes feed. The oviparous female may lay infertile eggs if not reached by a male, and these eggs do not become black. The fertile egg develops to the resting stage before the first heavy frosts; otherwise it may be winterkilled and will not hatch to a stem mother the following spring.

GENEALOGICAL DIAGRAM

The accompanying diagram (fig. 4) shows the number of lines possible from one stem mother as indicated by the writers' breeding experiments. A line from each form reproduced in any given generation from known parents was carried until the sexual forms appeared. In some cases the lines indicated either died or were lost. The former are shown by a short transverse line (–) and the latter by (?). It will be seen from the chart that one direct wingless line was obtained from the stem mother

and that a similar wingless line was obtained from the winged offspring of the stem mother. No direct winged line was obtained, and in those where winged individuals were in some numbers intermediates usually occurred also. Each large circle in the chart represents a generation.

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PLATE LXVII

Forms of *Aphis pomi:*

Fig. 1.—Winged viviparous female.
Fig. 2.—Male.
Fig. 3.—Pupa.
Fig. 4.—Oviparous female.
Fig. 5.—Wingless viviparous female.
Fig. 6.—Intermediate.

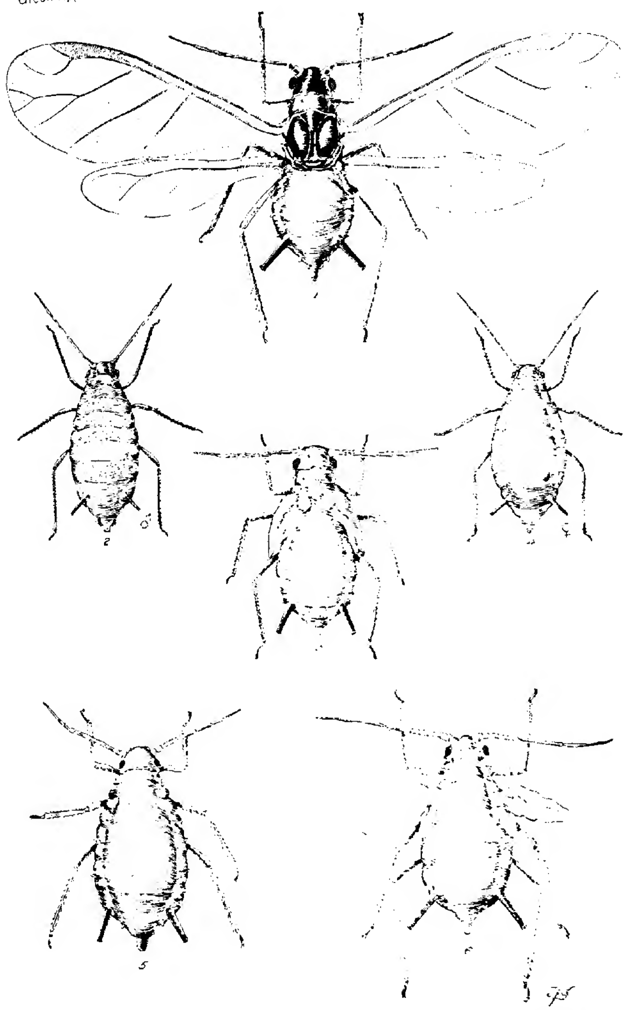

PLATE LXVIII

Embryology of *Aphis pomi:*

Fig. 1.—Fertilized egg previous to formation of blastoderm.

Fig. 2.—Fertilized egg showing formation of blastoderm.

Fig. 3.—Unfertilized egg.

Fig. 4.—Polar organ.

Fig. 5.—Condition of embryo and polar organ at commencement of revolution.

Fig. 6.—Yolk cell.

Fig. 7.—Germ cell.

PLATE LXIX

Embryology of *Aphis pomi:*

Fig. 1.—Ovarian yolk before division.

Fig. 2.—Half of ovarian yolk shortly after "dumb-bell" formation.

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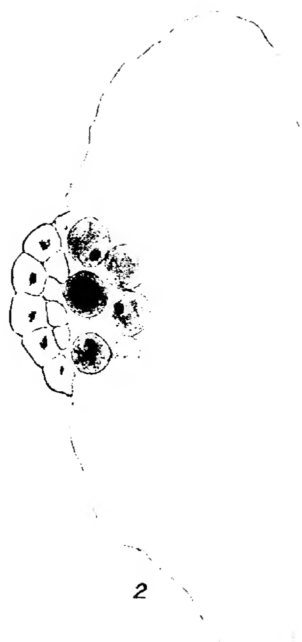

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PLATE LXX

Embryology of *Aphis pomi:*

Fig. 1.—Half of ovarian yolk, end chambers forming.
Fig. 2.—Half of ovarian yolk, end chambers formed.

PLATE LXXI

Embryology of *Aphis pomi.*

Fig. 1.—Half of ovarian yolk, egg chambers forming; condition at time of hatching.
Fig. 2.—Thickening serosa accompanied by cells of polar organ.

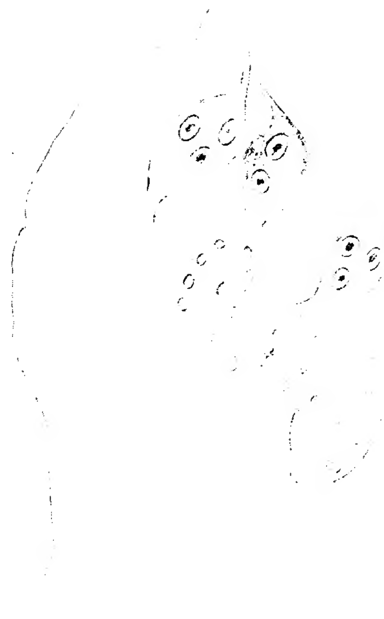

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PLATE LXXII

Embryology of *Aphis pomi:*

Fig. 1.—Invagination of dorsal body.
Fig. 2.—Dorsal body completely formed.

PLATE LXXIII

Embryology of *Aphis pomi:* Emerging nymph, showing egg burster.

PLATE LXXIV

PLATE LXXIV

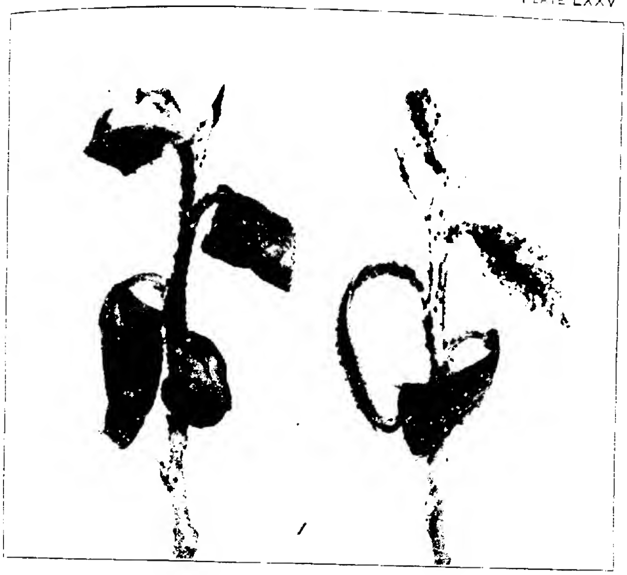
Structural details of *Aphis pomi*, *A. avenae*, and *A. malifoliae:*

Fig. 1.—*Aphis pomi:* Antenna of wingless viviparous female, adult.
Fig. 2.—*A. pomi:* Antenna of wingless viviparous female, third instar.
Fig. 3.—*A. pomi:* Antenna of wingless viviparous female, second instar.
Fig. 4.—*A. pomi:* Antenna of wingless viviparous female, first instar.
Fig. 5.—*A. pomi:* Antenna of stem mother.
Fig. 6.—*A. pomi:* Antenna of intermediate.
Fig. 7.—*A. pomi:* Antenna of winged viviparous female.
Fig. 8.—*A. pomi:* Male genitalia.
Fig. 9.—*A. pomi:* Antenna of male.
Fig. 10.—*A. pomi:* Antenna of wingless viviparous female, fourth instar.
Fig. 11.—*A. pomi:* Cornicle of winged viviparous female.
Fig. 12.—*A. pomi:* Cornicle of wingless viviparous female.
Fig. 13.—*A. pomi:* Cornicle of male.
Fig. 14.—*A. pomi:* Cornicle of oviparous female.
Fig. 15.—*A. avenae:* Antenna of stem mother, first instar.
Fig. 16.—*A. pomi:* Antenna of stem mother, first instar.
Fig. 17.—*A. malifoliae:* Cornicle of winged viviparous female.
Fig. 18.—*A. avenae:* Cornicle of winged viviparous female.
Fig. 19.—*A. pomi:* Cauda of adult.
Fig. 20.—*A. pomi:* Hind tibia of oviparous female.
Fig. 21.—*A. pomi:* Cauda of pupa.

PLATE LXXV

Aphis pomi on its host plant:

Fig. 1.—Colonies on apple.
Fig. 2.—Apple twig bearing eggs.



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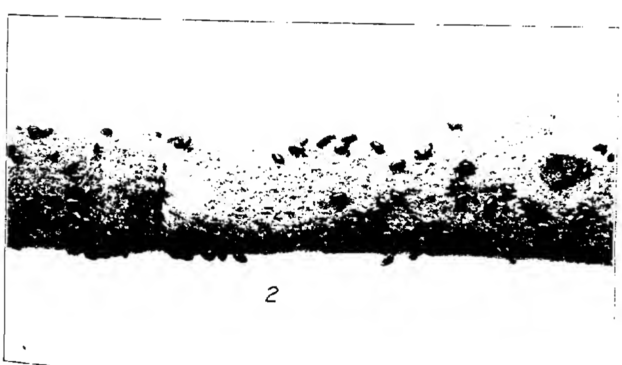

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SOILSTAIN, OR SCURF, OF THE SWEET POTATO[1]

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INTRODUCTION

Soilstain of the sweet potato (*Ipomoea batatas*) is a disease which is little known. The present work is the result of three years' investigations by the writer.

The disease was first described by Halsted (3) in 1890 under the name "scurf." For the last 24 years nothing new has been added to our knowledge of this trouble; subsequent writers have merely quoted Halsted. From the writer's studies (8, 9) it became evident that the disease needed further elucidation. The average grower little suspects that "stain" is a fungus trouble. In fact, the term "soilstain" as applied by the grower indicates his belief that there is something in the soil which stains the roots. He even believes that the plant itself leaves some coloring matter in the soil which stains subsequent crops of this valuable root. Others think that the staining is due to the application of manure to the soil; hence, they term it "manure stain."

ECONOMIC IMPORTANCE OF THE DISEASE

Soilstain is not a disease to be feared in the sense that it may produce a direct rot in the mature roots; nevertheless, it is economically important. Growers whose lands are badly infected assert that stained roots keep better in storage. Others find consolation in saying "there is no such thing as stain, the dark color of the skin being merely a varietal characteristic." The fact remains, however, that many eastern markets discriminate against stained roots. In years of overproduction the New York market refuses stained roots. The western buyers, on the contrary, are lax on this point; otherwise, many growers in the United States would be forced to cease producing sweet potatoes for want of a market.

OCCURRENCE OF SOILSTAIN

Soilstain is prevalent in Delaware on practically all sweet-potato land. It has also been reported from other States where sweet potatoes are grown. The writer has met with it in the sweet-potato districts of Delaware, New Jersey, Maryland, and Virginia.

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[1] The Editorial Committee of the Journal of Agricultural Research kindly forwarded to the writer a copy of Harter's paper on "Sweet-Potato Scurf" before it was published, with the suggestion that reference to that article be made. The writer has covered certain studies on the scurf of the sweet potato in storage and has treated more fully the morphology and physiology of the fungus than has Harter. These studies verify the work of Harter with one exception; in the morphology of the fungus he overlooked the fact that the conidia are catenulate.

[2] The writer is indebted to Dr. Charles Thom, of the Bureau of Chemistry, and Mrs. Flora W. Patterson, of the Bureau of Plant Industry, for having examined specimens of this fungus.

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SYMPTOMS OF SOILSTAIN

Soilstain is characterized at first by small, circular, deep-clay-colored spots on the surface of the sweet-potato root. These spots occur singly, but usually there are several in a given area. When very numerous, the spots coalesce, forming a large blotch which sometimes takes the form of a band or may cover the entire root. Soilstain is particularly conspicuous on the white-skinned varieties, such as the Southern Queen. Here the color of the spots is that of a deep-black clay loam. On the darker-skinned varieties the color of the spots does not appear so conspicuous. Soilstain is a disease of the underground parts of the plant. The vine and foliage are never attacked as long as they remain free from the soil. However, when these are covered, the petioles as well as the stems become infected.

EFFECT OF THE DISEASE ON THE HOST

After several months of storage, badly affected roots become a deep brown, which greatly contrasts with noninfected sweet potatoes. Occasionally, badly stained roots seem to be subject to more rapid drying and shrinking. This, however, is not often the rule. Usually soilstain is very prevalent in overheated storage houses. It may be, therefore, that the rapid shrinkage is due to the overheating and not to the effect of the disease itself. More data are necessary to determine these points. Soilstain is not only a disease of the epidermis (Pl. LXXVII, fig. *a*) and as such considerably reduces the market value of mature roots, but it also attacks the very young rootlets, preventing their further development and indirectly reducing the yield. In badly affected fields the writer has estimated a loss of 10 per cent of the crop from rootlet infection.

FACTORS FAVORABLE TO SOILSTAIN DEVELOPMENT

The type of soil seems to be a determining factor in the development of soilstain. Sweet potatoes grown on very light sandy soils, especially those which are hilly, are usually free from the disease. The heavier lands, or those rich in humus, rarely produce a clean crop. The application of manure favors the spread of the fungus and increases the stain. In fact, the manure itself is often a carrier of the disease, since diseased roots of all sorts find their way ultimately to the manure pile. The trouble is also carried directly with the seed stock. These, when planted in the seed bed, will produce 100 per cent of diseased sprouts. Experimental data, as well as extensive observations in seed beds and in the field, all corroborate these statements. Wet weather is favorable to the spread and increase of stain. During wet seasons the disease is more plentiful than in dry seasons.

STORAGE EXPERIMENTS

Growers who do not suspect the fungous nature of soilstain are always at a loss to explain the appearance of the trouble in storage when otherwise healthy roots are brought in. In order to determine definitely the effect of storage on this disease, the following experiments were carried out during two consecutive seasons: At digging time in September, 1913, a diseased field was chosen for that purpose. A large number of roots were selected and placed in hampers in the following ways.

Experiment 1.—Three hampers were filled with roots which to all appearances were free from stain. The object of the experiment was to determine whether apparently clean roots taken from a diseased field will develop stain.

Experiment 2.—Three hampers were filled with roots which showed very slight infection. The spots in these cases varied from 5 to 10 in number and were single and scattered. The object of this experiment was to determine whether the disease would increase in storage and the spots coalesce.

Experiment 3.—Three hampers were filled with roots which were thoroughly stained all over. The object of this experiment was to determine whether badly affected roots would be subject to more rapid drying and shrinkage.

Experiment 4.—Three hampers were filled with well-stained roots. At the bottom was placed a layer of stained roots, followed by a layer of healthy ones, on top of which was another layer of stained roots. Each layer was separated from the other by a narrow strip of paper. The object of this experiment was to determine whether healthy roots in contact with diseased ones will become infected under storage conditions.

Experiment 5.—Three hampers were filled with roots which to all appearances were free from stain and were taken from an adjoining clean field. These were to serve as checks.

All the experimental hampers were placed in a medium-sized potato house which had poor facilities for ventilation. The conditions, therefore, were ideal for the experiment. The hampers were stored for a period of 5½ months.

The results of the above experiments may be summarized as follows: The roots in the first three hampers (experiment 1) remained clean, indicating that clean roots, though coming from an infected field, when stored and protected from contact with stained roots, will remain clean. The roots in the second three hampers (experiment 2) showed an increase in the stain and a coalescence of previously smaller spots. The roots in the third three hampers (experiment 3) seemed to be shrunken most. The roots in the fourth three hampers (experiment 4) indicated that apparently healthy potatoes may become stained when placed directly in contact with diseased roots. The check roots (experiment 5) were all free from stain. The above experiments were repeated in 1914 and 1915. The results obtained did not differ from those referred to above.

CAUSE OF SOILSTAIN, OR SCURF

Halsted (3) was first to attribute the cause of soilstain (scurf) to a fungus, *Monilochaetes infuscans* E. and H. However, Halsted and the later writers have left no record of having experimentally proved the pathogenicity of the fungus. The writer has found no records of its having been grown in pure cultures. Several efforts by the writer to obtain the organism from badly stained roots which were kept in storage at first yielded negative results. Each time the causative fungus was overrun by a varied and rapidly growing flora. Pure cultures of the fungus were finally obtained from plantings of young minute spots. Of 300 such spots, 10 per cent yielded colonies of the causative organism, and these were few in number. The plates were examined every day and it was found that the fungus did not appear until nearly three weeks after culturing. Because of this slow growth, the fungus in previous work was overrun by secondary invaders. The cultural work emphasized the necessity of making a large number of poured plates when working with an apparently difficult organism. The first reference to the fact that this fungus had been grown in culture was made by the writer (8, 9) in 1914 and also recently by Harter (4). Using pure cultures of the fungus, the writer reproduced the disease several times at will.

MORPHOLOGY AND PHYSIOLOGY OF THE FUNGUS

It has been stated that Halsted first named the organism. Although some figures are recorded in Halsted's bulletin (3), yet they are only fragmentary and do not take account of all the various stages of the morphology of the fungus. Halsted's observations of the fungus must have been limited to material on the host. In pure culture the fungus grows very slowly. It is characterized by small darkish round colonies (Pl. LXXVI, fig. 1) varying from one-tenth to one-fifth of an inch in diameter. The growth is floccose at the top, and anastomosed below, having a resemblance to a stroma in the substratum of the medium. The surface growth of a colony resembles that of species of Alternaria and some species of Cladosporium, but differing from these by its restricted slow growth. The surface of the colony of *M. infuscans* has an ashen color, which is also the general appearance of the fruiting. The fungus grows better on vegetable plugs and is at its best on steamed onion and celery stalks. The aerial mycelium is branched, septate, and hyaline when young (Pl. LXXVII, *n*, *w*). With age the mycelial cells turn gray, then black, and become filled with oil globules (Pl. LXXVII, *l*, *r*). The submerged hyphæ are made up of smaller cells which in old cultures swell and take on the appearance of chlamydospores. The conidiophores are distinct from the mycelium (Pl. LXXVII, *a*), and not obsolete, as stated by Stevens (7). From extended observations it was found that conidiophores do not arise in clusters, but are always formed singly

(Pl. LXXVII, *a, t, u*). They are erect, not branched, and when viewed hastily would be mistaken for setæ of species of Colletotrichum or Vermicularia. Upon a close examination they are found to be made of closely septate dark-celled mycelium, the base of which rests on one or two smaller ones (Pl. LXXVII, *a*). Generally the measurements of the conidiophores vary with the medium used. The host, too, seems to have a determining influence.

In material collected at random from the market or direct from storage the conidiophores appear to be smaller than those taken from artificially infected sweet potatoes. In the latter case, the causative organism seems to possess more vigor, because of moisture under control methods. The average of nearly 500 measurements on various media and on the host shows that the conidiophores vary from 100 to 300μ in length. Great difficulty was experienced in studying the formation of conidia. It is difficult to observe spore formation on storage material. Harter (4) claims that there is but one conidium formed at one time at the tip of the conidiophore. As soon as this conidium breaks off, a new one is formed in its place. The studies of the writer on this point are at variance with those of Harter. The writer finds that the spores are borne in distinct chains. In pure culture the chains break up very readily when moistened and pressed down with a cover glass. The spore chains break immediately when moistened with alcohol, oil, or any other liquid (Pl. LXXVI, fig. 2, *k, d, b*). The chains of spores do not appear to be held together with any kind of mucilage. However, it was found that when a dry cover glass is carefully placed on the surface of a colony growing in a Petri dish and the latter placed under the microscope, all the stages of spore formation could be studied with much ease. The spores are borne in chains (Pl. LXXVI, fig. 2, *a, i*, and LXXVII, *g, h*). At first, the protoplasm of the tip of the conidiophore is seen to round up, then a minute bud pushes out (Pl. LXXVII, *c*) and increases in size until a mature spore is developed, which is left standing at the tip of the conidiophore (Pl. LXXVII, *d*). All the succeeding newly formed conidia are formed at the tip of the conidiophore, so that the oldest conidium stands at the farthest end of the chain (Pl. LXXVII, *e, f, i*). Careful observations of these chains have shown them to be made up of from 10 to 28 conidia. A distinct characteristic of the latter is that they are always guttulate (Pl. LXXVII, *m*), irrespective of the medium used. In some cases the conidia in pure culture appear to be massed in "pockets" around the tip of the conidiophore, as in species of Gloeosporium or Fusarium (Pl. LXXVI, fig. 2, *c, e, g, h, j*). However, a close examination will show that this is no definite characteristic of the fungus.

It has been stated that the least disturbance will cause the chains of conidia to break up. In so doing they invariably cluster around the conidiophore, grouping themselves in various ways (Pl. LXXVI, fig. 2,

b, c, d, e, f, g, h). This is observed only when the fruitings of the fungus are seen in a dry state. However, when placed in a drop of water or in any other liquid, the chains of spores break up and scatter over the liquid. The spores (conidia) are 1-celled, hyaline, with a greenish tinge, but never dark or brown. They measure from 15 to 20 by 4 to 6μ. Sometimes a germ tube is produced at the tip of the conidiophore which later bears spores (Pl. LXXVII, fig. *h, j, k, o, p*). Broken-off mycelial cells are also capable of germinating. In this case a germ tube upon which spores are formed is first produced (Pl. LXXVII, fig. *b*). The spores readily germinate in water or in any nutrient medium (Pl. LXXVII, fig. *m, q, s, v, x, y, z*).

An attempt was made to determine whether *M. infuscans* would also cause a rot of the interior of the sweet-potato root. Inoculations made with pure cultures of the fungus in slits made with a sterilized and cooled scalpel showed the organism incapable of causing a rot of the root. It was thought that perhaps the starch or the sugar was detrimental, but the fungus grows well on a starchy medium prepared according to Smith (6, p. 196), although not so well on media rich in sugar. It seems probable that neither the sugar nor the starch restricts the growth of the organism to the epidermis only, but this is done by the enzyms of the host.

TAXONOMY OF THE FUNGUS

The name "*Monilochaetes infuscans*," meaning black bristly Monilia, given by Halsted to the soilstain fungus, remarkably describes the main features of the organism. However, Halsted failed to describe fully either the species or the genus. Saccardo (5) barely mentions the fungus. Neither Engler and Prantl (2) nor Clements (1) nor any other systematic writer on fungi record the genus Monilochaetes. The description given by Stevens (7, p. 597) is incomplete. It was probably taken from naturally infected material, where the chains of conidia are seldom, if ever, noticed, since they are partially broken off with the rubbed epidermis. The conidiophores in such material are often broken down or wanting. From the present studies it seems that the writer is warranted in retaining the names of both the genus and the species of Monilochaetes as used by Halsted. Harter (4), too, decided to retain this genus. The description from a pure culture follows.

Monilochaetes infuscans E. and H.

Spores borne in chains which readily break up; conidia hyaline to greenish, guttulate; conidiophores black, several septate; mycelium first hyaline, then darker with age. The submerged mycelium swells irregularly. Conidiophores, 100 to 300 by 3 to 7μ; conidia, 15 to 20 by 4 to 6μ. The fungus is a very slow grower on artificial media. Parasitic on the sweet-potato root, causing a brown, blotched disease of the epidermis.

SUMMARY

Soilstain, or scurf, is a disease of the epidermis of the sweet-potato root. The disease occurs in every sweet-potato section, East and South, and is probably generally distributed. It is more abundant in the heavier soils, especially where manure is used as a fertilizer.

Soilstain reduces the market value of the mature roots. It reduces the average yield by attacking also the younger rootlets and stunting their development.

Soilstain is a disease of the underground parts of the plant. In storage the disease spreads by contact and is favored by moist, poorly ventilated houses.

The fungus *Monilochaetes infuscans* is difficult to culture, because it is a very slow grower and is readily overrun by associated saprophytes. The conidiophores of *M. infuscans* are distinct from the mycelium, the older growth of which is also dark. The conidia are borne in chains which readily break up when moistened or disturbed.

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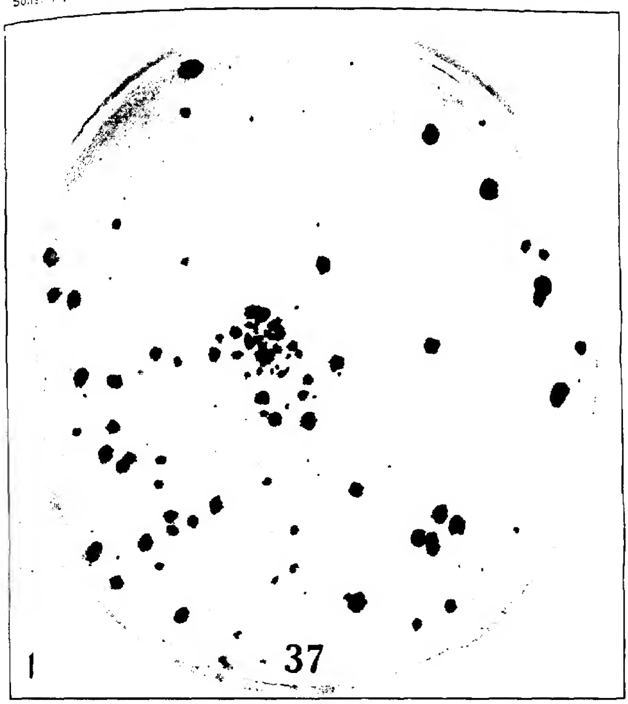
PLATE LXXVI

Fig. 1.—Petri dish containing a pure culture of *Monilochaetes infuscans*.

Fig. 2.—*a*, Part of a conidiophore of *M. infuscans*, showing the unbroken chain of conidia; *b*, *d*, and *k*, various ways of the breaking up of the chains of conidia when disturbed or moistened; *c*, *e*, *f*, *g*, *h*, and *j*, spores collecting in pockets after the chains of conidia have broken up; *i*, bending in of the chain of conidia prior to breaking up into individual spores.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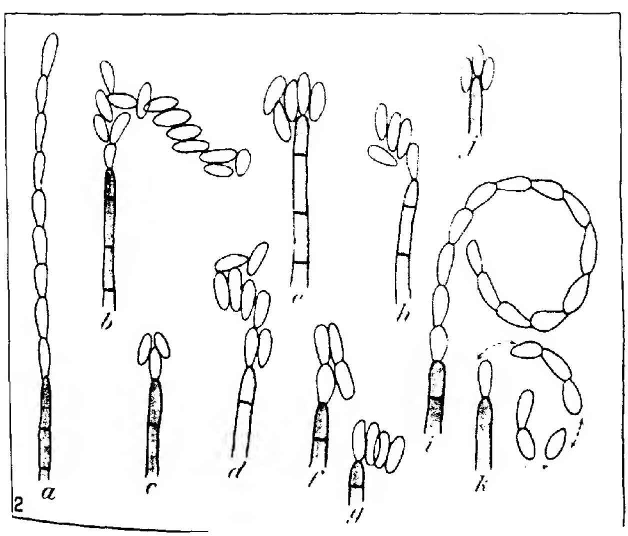
2
a
b
c
d
k

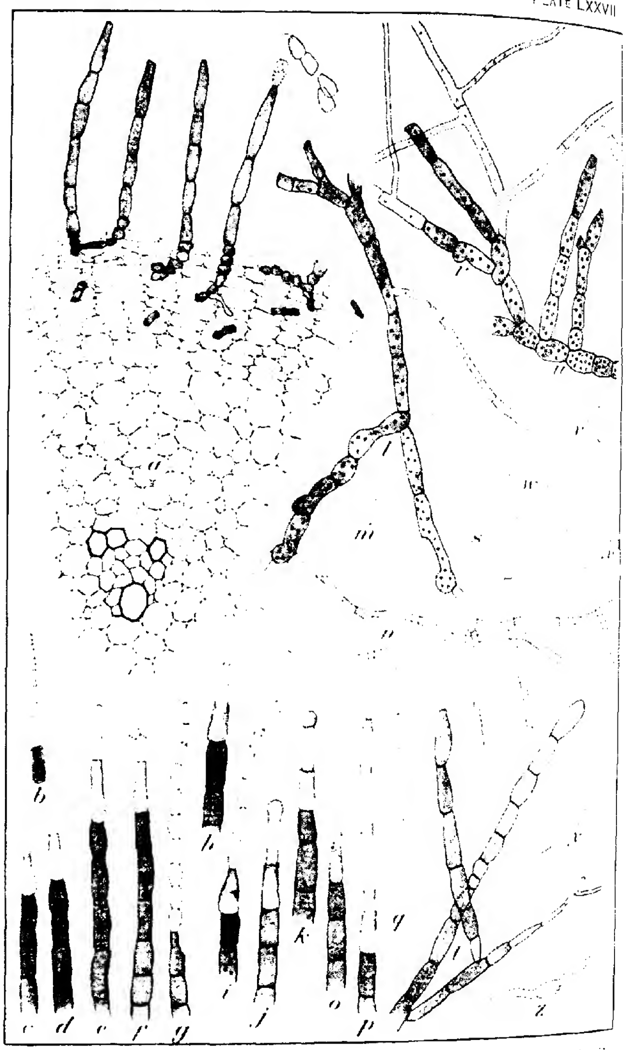
a
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PLATE LXXVII

a, Part of a cross section of a sweet-potato root, showing the relationship of *Monilochaetes infuscans* to the epidermis of the host;

b, Germination of a fragment of mycelium of *M. infuscans*, showing the germ tube which is first produced and upon which conidia are borne;

c, *d*, *e*, *f*, *g*, *h*, *i*, and *t*, Different stages in the development of the spore and the chain of conidia;

o, *j*, *k*, and *p*, Protruding hyaline tube at the tip of the conidiophore on which are borne the conidia; this form of fruiting is not common;

l, *n*, and *w*, Differentiation of the coarser dark mycelium, and the finer hyaline to subhyaline hyphæ;

u, Attachment of the conidiophore to the mycelium;

r, Conidiophore-bearing mycelium, being part of *u*;

m, *q*, *s*, *v*, *x*, *y*, and *z*, Different stages in the germination of the conidia of *M. infuscans*.